The evolution of human diversity

A phylogenetic approach

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Abstract

The socio-ecological correlates of cross-cultural variation in lactase persistence, sexual dimorphism in stature, and wealth inheritance in Africa were investigated, using phylogenetic comparative methods to control for the non-independence of populations (Galton's problem). Felsenstein's method of comparative analysis using independent contrasts, and Pagel's phylogenetic maximum likelihood model, were used. Genetic and linguistic trees were used as models of the past relationships among populations.

Lactase persistence was found to be associated with pastoralism but not with solar intensity or aridity. This is consistent with the hypothesis that high lactose digestion capacity in adults is an adaptation to dairying. This result does not support the hypotheses that low solar radiation at high latitudes and aridity are additional selective pressures for lactase persistence. Cross-cultural variation in stature was associated with women's work. Women are taller, relative to men, in societies where women contribute more to subsistence. In Africa, patrilineal wealth inheritance is associated with pastoralism and polygyny. Patrilineal wealth inheritance is adaptive if inherited wealth benefits sons more than daughters, which is probably the case in both polygynous and pastoralist societies. It is hypothesised that matrilineal inheritance arises from wealth inheritance to daughters. Inheritance to daughters is adaptive if the additional benefits of wealth inheritance to sons do not outweigh the risk of paternity uncertainty of sons' offspring.

The transmission, between populations, of those bio-cultural traits in the comparative analyses was also investigated. The association between each trait in a population, and that trait in the population's phylogenetic sister-group and nearest geographical neighbour(s) were compared using regression. The majority of traits were found to be associated with phylogeny. Some traits showed an additional association with geographical neighbours. Vertical transmission, from 'mother' to 'daughter' populations, appears to be more important than geographical diffusion between neighbouring populations, for the majority of the traits tested here.

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Chapter 1

Introduction to biocultural adaptation and the comparative method in anthropology

1.0 Summary of chapter 1

The aims of the thesis are outlined. Concepts of adaptation and cultural evolution are introduced. Methods for testing adaptive hypotheses are discussed, including optimality models, experiments and the comparative method. When using the comparative method in anthropology, one faces the problem that cultures are ancestrally related, and so are not independent for the purposes of statistical analysis. This is known as Galton's problem. Comparative methods that control for the non-independence of populations are reviewed, including the phylogenetic methods used in this thesis. The transmission of biocultural traits between populations, and its implications for Galton's problem and the comparative method, are discussed. It is discussed whether humans are adapted to the environments they inhabit today. The contents of chapters 2-7 are outlined.

1.1 Aims of thesis

The first aim was to investigate the nature of the transmission of biological and cultural traits between human populations, specifically to determine whether the traits are transmitted vertically from 'mother' to 'daughter' populations, and/or by horizontal diffusion between neighbouring populations. This question is central to understanding processes of cultural evolution, and also affects the degree to which cultures can be treated as independent data points in a cross-cultural comparison. The second aim was to test adaptive hypotheses about the evolution of biocultural diversity in lactose digestion capacity in adults, wealth inheritance in Africa, and sexual dimorphism in stature, using comparative methods that control for the non-independence of populations (Galton's problem).

1.2 Adaptation and biocultural evolution

An adaptation is a feature of an organism which evolved in response to a specific natural selection pressure (Williams, 1966). This can include both genetic and phenotypic adaptation. In humans, cultural adaptation also occurs, meaning socially learnt behaviour which is adaptive, in the sense of increasing an individual's chance of survival or reproductive success.

In genetic adaptation, different phenotypes are associated with allelic variation among individuals. An example is lactose digestion capacity in adults (chapter 4). Two phenotypes exist, high and low capacity to digest lactose in adulthood. This character state is determined by a single genetic locus (Sahi et al., 1973; Ransome-Kuti et al., 1975; Johnson et al., 1977; Metneki et al., 1984). High lactose digestion capacity is thought to be an adaptation to herding livestock (Simoons, 1978; Holden and Mace, 1997).

In phenotypic adaptation, a single genotype produces different phenotypes, depending on the environment. This is sometimes called developmental (Bogin, 1999) or environmental (Boyd and Richerson, 1985) adaptation. Environmental conditions, especially during development, affect many aspects of the phenotype, such as growth rate and adult size (Bogin, 1999). The response of a genotype to environmental variation (determining the range of phenotypes) can be described by a function called the 'norm of reaction'. The norm of reaction is evolved and heritable. This type of phenotypic plasticity is adaptive, permitting an organism to respond adaptively to a variable environment during development and adulthood. Behaviour is an aspect of phenotypic plasticity, enabling an individual to respond adaptively to a variable or unpredictable environment (Hill and Hurtando, 1996).

Cultural behaviour is distinguished from other forms of animal behaviour because it is socially learnt, not genetically encoded. Different approaches to the study of cultural behaviour exist within evolutionary biology. These include the adaptationist approach of evolutionary ecology (e.g. Hill and Hurtando, 1996), and cultural

evolutionary theory, which focuses mainly on the transmission of cultural traits within and between populations (Cavalli-Sforza and Feldman, 1981; Cavalli-Sforza et al 1981; Richerson and Boyd, 1985; Richerson and Boyd, 1992).

Culture and evolutionary ecology. The primary argument of evolutionary ecology is that organisms are optimally evolved to maximise their reproductive fitness within their niche. This is a heuristic approach, in which apparently maladaptive traits are assumed to have an adaptive function that is not yet understood. Behavioural ecology, or sociobiology, refers to that part of evolutionary ecology which seeks to understand behaviour in its ecological context (Voland, 1998). Behaviour is assumed to be adaptive, like other aspects of the phenotype. The proximate mechanisms underlying behaviour (whether behaviour is genetic or learned) tend to be ignored as irrelevant to understanding a behaviour's adaptive function (Grafen, 1991; Richerson and Boyd, 1992; Hill and Hurtando, 1996). Cultural variation is treated as an aspect of phenotypic plasticity. Like other forms of behaviour, cultural behaviour can be adaptive, in the sense of increasing an individual's Darwinian fitness (e.g. Hill and Hurtando, 1996; Betzig, 1997). It is assumed that humans have an evolved propensity to adopt cultural behaviours that are adaptive, maximising their reproductive fitness (Cosmides et al., 1992; Richerson and Boyd, 1992; Hill and Hurtando, 1996). The capacity for culture is treated as an evolved adaptation, enlarging the possibilities of phenotypic adaptation to the environment (Feldman and Laland, 1996). The cultural context within which a person lives (i.e. the behaviour of other people) is treated as an aspect of the environment.

Cultural evolutionary theory. Cultural evolutionary theory focuses on how cultural traits are transmitted between individuals. The transmission of cultural traits has been modelled using mathematical models from population genetics, modified to incorporate horizontal modes of transmission, in which cultural traits are transmitted between unrelated individuals (Cavalli-Sforza and Feldman, 1981; Cavalli-Sforza et al., 1981; Boyd and Richerson, 1985). Models show that, because the transmission of cultural traits is not dependent on biological reproduction, maladaptive cultural behaviours have the potential to spread like infectious diseases. Evolutionary ecology and cultural evolutionary theory can therefore differ in their predictions about whether or not a cultural trait is adaptive for the person adopting that trait (Richerson and Boyd, 1992).

The adaptationist approach to cultural behaviour was used in this thesis. The 'adaptationist wager' has proven to be a useful research tool in evolutionary biology (e.g. Hamilton, 1964; Parker and Maynard-Smith, 1990; Grafen, 1991) including the study of human behaviour (e.g. Betzig et al., 1988; Borgerhoff Mulder, 1991; Smith and Winterhalder, 1992; Betzig, 1997).

1.3 Testing adaptive hypotheses

Adaptations can be recognised because they are well 'designed' by selection to solve particular problems in the environment. The function of a trait is inferred from its properties, leading to the formulation of hypotheses about the selection pressures that affect that trait (Williams, 1966; Grafen, 1991; Dennett, 1996). Adaptive hypotheses can be tested using experiments, optimality modelling and the comparative method (Harvey and Pagel, 1991). Experiments entail manipulating one aspect of the phenotype and/or the environment in order to assess the effects of altering a trait on some component of an organism's fitness (Sinervo and Basolo, 1996). Optimality approaches compare the observed values of a trait (either the population mean or the range of variation along a reaction norm) with predicted values that would be obtained if an organism were maximising some component of fitness such as energy intake (Maynard Smith, 1978; Krebs and Kacelnik, 1991).

In comparative analysis one uses naturally occurring variation between populations to test for a correlation between two characters, or between a character and an environmental variable. The aim is to test for instances of correlated evolution or convergence among variables (Harvey and Pagel, 1991; Mace and Pagel, 1994; 1997a). In this thesis, the comparative method was used to test adaptive hypotheses about the evolution of biocultural diversity.

1.3.1 The comparative method

The simplest method of cross-cultural comparison is to test for a correlation between two traits, or between a trait and an environmental variable, across populations (e.g. Tylor, 1889; Levinson and Malone, 1980; further examples are reviewed in chapters 4-6). The problem with this method is that hierarchically related populations (including human cultures) are not independent for the purposes of statistical analysis (Dow et al., 1984; Harvey and Pagel, 1991; Pagel, 1994; Mace and Pagel, 1994). This is known as Galton's problem, first pointed out by Sir Francis Galton in 1889, in a discussion of a classic cross-cultural analysis of kinship by E. Tylor:

> Mr Galton said that... full information should be given as to the degree in which the customs of the tribes and races which are compared together are independent. It might be, that some of the tribes had derived them from a common source, so that they were duplicate copies of the same original. Certainly... each of the observations ought, in the language of statisticians, to be carefully "weighted" (Galton, quoted in Tylor, 1889).

Treating populations as independent data points in a comparative analysis leads to an over-estimation of the number of independent cases, and of the degrees of freedom, tending to inflate the statistical significance of associations found within the sample. A background of ancestral dissimilarity among populations can also obscure real or functional relationships among variables (Dow et al., 1984; Harvey and Pagel, 1991).

Several methods have previously been used to control for Galton's problem in cross-cultural comparison. These include sampling methods (excluding closely related cultures from the sample, and 'controlled comparison') and autocorrelation analysis.

Excluding closely related cultures from the sample. In this method, closely related populations are excluded from the sample. This general sampling technique was called 'sifting' by Naroll (1961). Murdock and White's (1969) 'Standard cross-cultural sample' is the most widely used application of this method (e.g. Murdock and Provost, 1973; Broude and Greene, 1976; Gaulin and Schlegel, 1980; Wolfe and Gray, 1982a). The Standard cross-cultural sample was designed as a representative worldwide sample of 186 cultures, from which closely related cultures were excluded. However, excluding closely related populations from the sample does not eliminate similarities among populations inherited from more distant ancestors. Moreover, it results in the loss of potentially informative variance among closely related populations, thereby increasing the likelihood of Type II errors (failing to detect real patterns in the data) (Naroll, 1961; Mace and Pagel, 1994).

Controlled comparison. In controlled comparison, only closely related cultures are included in the sample, ideally cultures which differ in only one variable of interest, forming a natural experiment (Eggan, 1961). For example, Goodenough (1957) compared Polynesian populations which inhabit coral reefs and high islands. Again, one problem with this method is that the sample size is likely to be small. Further, in any sample of cultures larger than two, it is likely that some cultures in the sample are more closely related than others are. Hierarchical relationships among relatively closely related cultures are clearly seen in linguistic relationships (e.g. Kirch and

Green, 1987). Correlations among characters in the sample may therefore have historical rather than functional causes.

Network autocorrelation. White et al. (1981) and Dow et al. (1984) used network autocorrelation to control for Galton's problem. In network autocorrelation, the geographically diffused component of covariance among characters is removed, so that comparative analysis is performed on the residual values of the variance. This method differs from the phylogenetic methods used in this thesis, in that it does not use an explicit model of phylogeny, and it attempts to remove the effects of geographical diffusion of traits, rather than counting geographical diffusion as possible evidence of adaptation, as was done here (see below). An earlier, similar method, developed by Naroll (1961), measured the degree of clustering between character states in discrete binary variables.

A new approach to Galton's problem was proposed by Mace and Pagel (1994), the use of phylogenetic comparative methods from evolutionary biology.

Phylogenetic comparative methods. Phylogenetic comparative methods were developed in evolutionary biology to control for the effects of phylogeny among species. It was recognised by Darwin that, for the purposes of comparative analysis, species are not independent, because they are related by descent:

> An ancient progenitor may have acquired through natural selection some one modification in structure, and after thousands of generations, some other and independent modification; and these two modifications having been transmitted to a whole group of descendants with diverse habits, would naturally be thought to be correlated in some necessary manner (Darwin, 1859: 185).

Phylogenetic comparative methods control for non-independence among taxa by counting independent evolutionary events (or changes) as data, rather than character states within a sample (Gittleman, 1981; Ridley, 1983; Cheverud et al., 1985; Felsenstein, 1985; Harvey and Pagel, 1991; Pagel, 1992; 1994; 1998). The importance of identifying independent events in cultural evolution was also recognised by a number of anthropologists (for example by Goodenough, 1957, Kirch and Green, 1987). Mace and Pagel (1994; 1997a) suggested that the phylogenetic comparative methods developed in biology could also be used in cross-cultural comparison in anthropology, to control for non-independence arising from the historical relationships among populations (Galton's problem).

Two phylogenetic comparative methods were used in this thesis, comparative analysis using independent contrasts (Felsenstein, 1985; Pagel, 1992) and a method for testing for correlated evolution among discrete traits using maximum likelihood (Pagel, 1994). These methods are outlined below, and described in more detail in chapter 3.

Comparative analysis using independent contrasts. In this method, one tests for correlated evolutionary change in two characters, or in a character and an environmental variable (Felsenstein, 1985; Pagel, 1992). First a phylogeny (a tree showing the past relationships among populations) is constructed. For cross-cultural comparison this may be based on genetic or linguistic similarity (Kirch and Green, 1987; Mace and Pagel, 1994; Holden and Mace, 1997; see chapter 2). Character states at internal nodes of the tree (i.e. ancestral character states) are estimated from character states at the tips of the tree (i.e. in populations in the cross-cultural sample).

Instances of evolutionary change in characters along the branches of the tree are counted as 'independent contrasts'. The relationship between independent contrasts in the variables hypothesised to be related is tested using standard statistical tests. Character change along any branch of the tree is independent of character change in any other branch, so there is no covariance among characters resulting from populations' shared ancestry (Felsenstein, 1985; Harvey and Pagel, 1991; Pagel, 1992; Mace and Pagel, 1994; 1997a). This method is described further in chapter 3, and was used in chapters 4, 5 and 6.

A method of testing for correlated evolution among discrete characters. This method tests for correlated evolution among discrete characters using maximum likelihood (Pagel, 1994). Character states in the variables hypothesised to be related are mapped onto a population phylogeny. Two likelihood models are fitted to the data, a model in which evolutionary change in the two variables is independent, and a model in which the likelihood of change in one variable is dependent on the state of the other. The log-likelihood (a measure of goodness of fit) of the independent model is compared to the log-likelihood of the dependent model. If the dependent model is significantly more likely, this is evidence that the two variables are correlated. This method can also be used to test which of two correlated traits probably evolved first. This method is described further in chapter 3, and was used in chapters 4 and 5.

1.4 The transmission of traits between populations

Phylogenetic models were developed to test adaptive hypotheses across species. To apply these methods at the population level, populations need to be hierarchically related in a tree-like pattern. The extent to which this is true of human populations is discussed in chapter 2, where it is concluded that trees based on genetic and linguistic similarity among populations can be used as models of human population history.

Across populations, gene flow and cultural diffusion are possible, in contrast to species, across which there is no gene flow (Mayr, 1963). In the phylogenetic methods used in this thesis, gene flow and cultural diffusion are treated as statistically equivalent to independent evolution. If two traits are consistently adopted together (from neighbouring populations), or if one trait is consistently adopted from neighbouring populations in association with an environmental variable, this is evidence that the two variables are functionally related (Naroll, 1961; Mace and Pagel, 1994). For example, Mace and Pagel (1994) showed that in East Africa, populations migrating into an arid area adopted camels from existing dryland populations, evidence that camel pastoralism is adaptive in these areas.

One aim of this thesis was to estimate the relative importance of vertical and horizontal transmission for biocultural traits. Understanding the transmission of bio-

cultural traits among populations is important for using phylogenetic comparative methods in cross-cultural comparison for a number of reasons. First, the statistical methods used to estimate past character states on a tree are based on the assumption that most characters are transmitted vertically (Felsenstein, 1985; Pagel, 1992). This assumption can be tested empirically for different bio-cultural traits. If traits are inherited vertically, then one can have more confidence that the reconstruction of past character states on phylogenies is realistic.

Second, the lability of a trait affects the degree to which it is associated with population history: Galton's problem is worse for traits which are highly conserved in transmission. It has been argued that cultural characters are so labile that it is not necessary to control for the effects of phylogenetic inheritance (e.g. Thornhill, 1991; Cashdan and Rogers, 1997; Rogers and Cashdan, 1997). However, Galton's problem does not arise only in relation to phylogenetically constrained characters. Spurious statistical associations among functionally unrelated traits, resulting from the inheritance of multiple traits from a common ancestor, can also occur among cultural traits (Dow and Pollock, 1991; Mace and Pagel, 1994; 1997a; 1997b). One should therefore test the claim that cultural traits are highly changeable. It can be shown empirically that there is a strong association between most cultural traits and population history (Guglielmino et al., 1995; chapters 4-6), leading to the conclusion that controlling for phylogeny is necessary when testing adaptive function in these traits cross-culturally.

The mode of transmission of cultural traits is also a central question in many other areas of archaeology and anthropology, for example, in understanding the spread of

agriculture across Europe at the beginning of the Neolithic (Ammerman and Cavalli-Sforza, 1984; c.f. Zvelebil, 1995).

Concepts and methods used to study the nature of the transmission of traits among populations are reviewed below, along with the results of empirical studies.

The unit of cultural transmission. In biological evolution a distinction is made between the phenotype and the gene. Only genes are transmitted in biological reproduction. It has been argued that in cultural transmission, 'memes' (Dawkins, 1976), analogous to genes, are transmitted between individuals (Dennett, 1996). Memes are defined as units of information (ideas or beliefs), encoded in language or other symbolic systems, which prescribe the form of a behaviour or artefact (Durham, 1991). An individual meme is the largest unit of information which is transmitted intact between individuals. Dawkins (1976: 206) suggested that 'tunes, ideas, catch-phrases, clothes fashions, ways of making pots [and] of building arches' constituted memes. Dennet (1996: 344) defined memes as: 'the sort of complex ideas that form themselves into distinct memorable units', such as 'arch, wheel, wearing clothes, vendetta, right triangle, alphabet, calendar, the Odyssey, calculus, chess, perspective drawing, evolution by natural selection, impressionism, Greensleeves, deconstructionism'. Lake (1998) noted that memorability is a characteristic of successful memes only, which are replicated with a high degree of fidelity, and which give rise to recognisable cultural lineages. The transmission of memes is contrasted with genetic transmission in Table 1.1.

Table 1.1 Differences between memes and genes

Property	Memes	Genes
Basic properties	Coded information, expressed in behaviour or artefacts manufactured by carriers of this information	Coded information, expressed in the phenotype
Code	'Mental code', not understood	Genetic code
Source of variation	Innovation / invention	Mutation
Storage	In individual's memories, written texts or other stores of cultural information	DNA
Mechanism of transmission	By social learning between individuals; also transmitted through written texts and other stores of cultural information.	Biological reproduction
Patterns of inheritance	Between individuals, often parents and children, but not necessarily. Transmission between unrelated individuals possible. Simultaneous transmission from one person to many possible.	Mendelian

It is unclear how far 'memes' are really involved in cultural transmission, or whether cultural transmission is more similar to a Lamarkian process of direct imitation from the phenotype (Lake, 1998). Pétrequin (1993) described a probable case of the transmission of a meme for 'flat-bottomed pots' among Alpine cultures dated at 3700 BC to 2400 BC. In this unusually well dated sequence of archaeological remains, the idea of 'flat-bottomed pots' appears to have been transmitted to a population which previously had only produced round-bottomed pots, without the simultaneous transmission of the technique for producing a flat-bottomed pot. The technique for producing flat-bottomed pots was then reinvented by trial and error over two or three generations. This historical sequence suggests that a meme for 'flat-bottomed pots' existed independently of the actual pot-making process (Lake, 1998).

Many authors (e.g. Cavalli-Sforza et al., 1981; Boyd and Richerson, 1985) have not made a strict distinction between memes and behaviours (analogous to the distinction between the genes and the phenotype) when studying cultural transmission. Empirically, memes can only be identified when they are manifested in artefacts or forms of cultural behaviour, which are called cultural traits. Hewlett and Cavalli-Sforza (1986) treated skills like 'find mushrooms', 'net hunt' and 'carry infant in a sling' as cultural traits in an analysis of cultural transmission in Aka Pygmy foragers in central Africa. Guglielmino et al. (1995) treated the variables in Murdock's (1967) *Ethnographic Atlas* as cultural traits. Variables in the *Ethnographic Atlas* were also treated as cultural traits in this thesis (chapters 4, 5 and 6).

The rate of change in cultural traits. As previously noted, the rate of change in cultural traits affects the degree to which cultures can be treated as independent, in

other words, the severity of Galton's problem in cross-cultural comparison. It is often assumed that cultural traits are highly changeable, in contrast to genetic traits. It is true that cultural traits are *capable of* rapid change. However, cultural traits may also be transmitted with a variable degree of fidelity. The fidelity of cultural transmission can be high if the cultural trait is adaptive. For example, cattle-keeping and associated aspects of material culture in the Sahel-Sudan region have retained similarities from ca. 8000 BC to recent times (Ehret, 1993; c.f. Evans-Pritchard, 1940). The cultural variation observed today has a long history of 'descent with modification' (c.f. Darwin, 1859) from earlier cultures (Durham, 1991; Mace and Pagel, 1994; Gugielmino et al., 1995). Cultural inheritance in human populations is analogous to phylogenetic inheritance in species. If two individually adaptive cultural traits are retained in a population and its descendants over millennia, this does not necessarily indicate that the two traits are functionally related.

Conservatism in traits is adaptive in environments where there is little change from generation to generation, enabling an optimal strategy to emerge. Genetically based behaviour, which is less labile than cultural behaviour, is adaptive in very stable environments. In more rapidly changing environments, a greater rate of innovation is adaptive, enabling individuals to track environmental changes. The capacity for cultural behaviour enables humans to respond more rapidly to a changing environment (Feldman and Laland, 1996; Richerson and Boyd, 1992). (Note that in a very unpredictable environment, individual learning by trial and error can be more adaptive than cultural learning, because inherited information will be quickly out of date, Feldman and Laland, 1996). Different types of cultural transmission may also be associated with variation in the degree of cultural conservatism. Cavalli-Sforza and

Feldman (1981) and Cavalli-Sforza et al. (1981) suggested that many-to-one transmission, such as initiation of adolescent initiation by tribal elders, is the most conservative type of cultural transmission. One-to-one cultural transmission, typically from parent to child, is a moderately conservative mode of transmission. One-to-many transmission such as classroom teaching is potentially the least conservative type of cultural transmission, permitting the rapid adoption of cultural innovation (see Table 1.2).

Table 1.2 Cultural transmission and innovation (adapted from Hewlett and Cavalli-Sforza, 1986)

	Modes of cultural transmission			
	Vertical	**Horizontal**	**One-to-many**	**Many-to-one**
Transmitter	Parent(s)	Unrelated	Teacher/leader/ media	Older members of the social group
Transmittee	Child	Unrelated	Pupils/citizens/ audience	Younger members of the social group
Acceptance of innovation	Intermediate difficulty	Easy	Easy	Very difficult
Cultural evolution	Slow	Can be rapid	Most rapid	Most conservative

Studies of cultural transmission within cultures. Hewlett and Cavalli-Sforza (1986) studied cultural transmission in a group of 40 Aka Pygmy foragers in the central African rainforest. They investigated the transmission of fifty skills relating to subsistence, reproductive behaviour, childcare, and dancing and singing. They asked Aka individuals whether they possessed each skill, and if so, from whom they learnt this skill. Direct observations of parent-infant interactions were also made. Hewlett and Cavalli-Sforza found that parent-to-child transmission was by far the most important type of cultural transmission, accounting for about 80% of cases of cultural

transmission. Crossbow hunting (a recent innovation) and dancing and singing (communal group activities) were the only cultural traits which a large number of people had learnt from non-parents. Cavalli-Sforza et al. (1981) investigated the transmission of a number of cultural traits in an American population. Using interviews and questionnaires, they tested for similarities among parents and children in beliefs and behaviours related to religion, politics, sports, leisure activities and daily habits (e.g. adding salt to meals, and drinking tea and coffee). They that found parents and children were more similar in their religious and political attitudes than in other cultural traits. The similarities among parents and children in other cultural traits also tended to be significant, but weaker. These results suggest a high degree of cultural transmission from parents to children. The strength of vertical relative to horizontal transmission varies across different cultural traits.

Studies of cultural transmission between cultures. Guglielmino et al. (1995) used quantitative methods to investigate the nature of transmission of 47 cultural variables among 288 African societies, using data from Murdock's (1967) *Ethnographic Atlas*. This is the by far the most comprehensive and rigorous study which has been done on cultural transmission. The 47 cultural traits they investigated are shown in Table 1.3.

Table 1.3 Cultural traits investigated by Guglielmino et al. (1995)

Type of trait	Traits included in this category
Family and kinship	Type of marriage, residence, family organisation, community organisation, patrilineal, matrilineal and cognatic kin groups, cousin marriage and terminology, property inheritance and rules for succession to the status of headman
Economy	Subsistence practices (gathering, hunting, fishing, pastoralism and agriculture), type of agriculture and animals, settlement pattern
Social stratification	Community size, within- and between-group hierarchy, class and caste stratification and slavery.
Sexual division of labour	Sexual division of labour for metal-working, weaving, leather-working, pottery, boat building, house construction, gathering, fishing, animal husbandry and agriculture.
House construction	Including details of floor, walls and roof.
'Various others'	Belief in god(s), games, post-partum abstinence and pre-marital sexual norms, male genital mutilations, segregation of adolescent boys.

Guglielmino et al. (1995) tested for three different processes, hypothesised to explain distribution of cultural variation in Africa:

1. Vertical transmission of cultural traits, from older to younger generations within populations
2. Geographical transmission of cultural traits between neighbouring populations
3. Adaptation to the environment.

They tested for vertical transmission (which they called demic diffusion) by testing whether cultural traits were associated with linguistic groups, assumed to be a marker of population history (Cavalli-Sforza et al, 1988; Barbujani, 1991; chapter 2). An association between a cultural trait and language group was thought to indicate that the trait was transmitted vertically, within populations. They tested for adaptation to the environment by testing whether traits were associated with ecological zones, defined from a map of Africa's vegetation. An association between a trait and an ecological zone was thought to indicate that the trait was an adaptation to a particular environment. They tested for geographical clustering using by calculating an index based on the ratio:

$$r = d/dS$$

where d is the distance of a population from its nearest geographical neighbour and dS is the distance of a population from the nearest neighbour with the same character state for a cultural trait.

Guglielmino et al. (1995) found that family and kinship, the economy, house construction and social stratification tended to show a strong association with

linguistic group, indicating vertical transmission (demic diffusion). The economy, social stratification and house construction showed some association with ecological zones. Overall, fewer cultural traits were associated with ecological zones than with linguistic groups. This may indicate that cultural inheritance is more significant than ecological adaptation in explaining the current distribution of cultural traits in Africa. One can question this conclusion, however, because ecological zones are a crude estimate of variation in the human environment. It would be preferable to test the correlation between types of subsistence and other cultural traits. For example, in chapter 5, evidence that patriliny is an adaptation to pastoralism is presented (see also Aberle, 1961). The sexual division of labour and 'various other' cultural traits (see above) showed a high degree of geographical clustering, indicating that they are transmitted by diffusion among neighbouring populations. One can criticise this test on the grounds that geography is not independent of cultural history: in other words, closely related cultures also tend to live close together. However, it is notable that the sexual division of labour and 'various other' cultural traits did not show an association with language group, which one would have expected if the geographical clustering were due to cultural ancestry. A summary of Guglielmino et al.'s (1995) results is shown in Table 1.4.

Table 1.4 Cultural transmission in Africa, a summary of Guglielmino et al.'s (1995) results

Type of cultural traits	Correlation with language group	Correlation with ecological zone	Degree of geographical clustering	Mode of transmission[1]
Family and kinship	High	Low	Low	Vertical
Economy	High	High	Medium	Vertical, horizontal and adaptive
Social stratification	Medium	Medium	Medium	Vertical, horizontal and adaptive
Sexual division of labour	Low	Low	High	Horizontal
House construction	Medium	Medium	High	Vertical, horizontal and adaptive
Various others (see Table 1.3)	Low	Low	High	Horizontal

[1] The three possible modes of transmission are vertical (within population), indicated by a correlation with language group; horizontal (between neighbouring populations), indicated by a high degree of geographical clustering; and adaptive, indicated by a correlation with ecological zone.

Pocklington and Breden (n.d.) also investigated the transmission of the same 47 cultural traits in a sample of 32 African cultures, a subset of Guglielmino et al.'s (1995) sample. They tested whether traits were transmitted vertically, from mother to daughter populations, or horizontally between neighbouring populations. They first constructed matrices of genetic, geographical and cultural distances among populations. Genetic distances were F_{ST} distances (see chapter 2), used as a proxy estimate of historical relatedness among populations. They tested for correlations between cultural distance, and genetic and geographical distances among populations. They used the Mantel matrix correspondence test, extended to compare more than two matrices using a multiple regression model (Smouse, Long and Sokal, 1986). This test enabled them to control for the confounding effect of historical relatedness and geographical proximity.

Pocklington and Breden did not test the mode of transmission for individual cultural traits, only for aggregate groups of traits. After controlling for the effect of geography, 'familial organisation' and 'social hierarchy' showed a highly significant correlation with genetic distance, indicating that these traits are transmitted vertically from 'mother' to 'daughter' populations. 'Familial organisation' included cousin marriage and terminology, inheritance of property and rules of succession to the status of headman. 'Social hierarchy' included class and caste structure, slavery, between- and within-group hierarchy, and the sexual division of labour for metal working and weaving. After controlling for the effect of historical relatedness (genetic distance), traits classified as 'religious practices' showed a significant correlation with geography, indicating that these traits are transmitted horizontally between neighbouring populations. 'Religious practices' included belief in god, presence of

games, post-partum abstinence, male genital mutilations, and segregation of adolescent boys. The importance of geographical diffusion in the transmission of religious practices contrasts with the findings of Cavalli-Sforza et al. (1981), who found that in an American population, religious beliefs were transmitted from parents to children. The presence of missionaries and conquests by Muslims and Christians in Africa might account for this difference. No other groups of cultural traits showed a significant correlation with either genetic or geographical distance. This may be because the populations in Pocklington and Breden's small sample (32 cultures, out of a cultural universe of several hundred African cultures) were not closely related.

Pocklington and Breden's aggregate groups of cultural traits differed somewhat from the groups used by Guglielmino et al. (1995), so their results cannot be compared in detail. However, cultural traits related to family organisation and kinship show a strong relationship with cultural ancestry in both studies.

The transmission of biological and cultural traits between populations was investigated in this thesis, using genetic and linguistic trees to estimate the past relationships among populations. Multiple and logistic regression were used to control for the confounding effects of history and geography. For each trait, character states in populations were regressed against character states in each population's geographical neighbours and phylogenetic relatives. An association with populations' phylogenetic relatives indicated that the trait was transmitted vertically, from mother to daughter populations. An association with populations' geographical neighbours indicated that the trait was transmitted by horizontal diffusion and/or is an adaptation

to the environment. Parallel evolution is an alternative but less parsimonious interpretation in each case. The method is described in more detail in chapter 3.

In chapters 4, 5 and 6 the transmission of the following biocultural traits was investigated: lactose digestion capacity (a genetic trait); pastoralism; sexual dimorphism in stature (probably a partially genetic character); the sexual division of labour; polygyny; and patrilineal and matrilineal inheritance. All traits were found to have a significant association with phylogeny, indicating that they are transmitted vertically, like traits among species. The sexual division of labour, level of polygyny, and pastoralism showed an additional association with geography, indicating either that these traits are also transmitted by horizontal diffusion or that variance in these traits is associated with environmental factors. More evidence of vertical transmission was found than was reported by Guglielmino et al. (1995) or Pocklington and Breden (n.d.). This was probably because more closely related groups of populations were compared.

In summary, many types of cultural trait are transmitted from 'mother' to 'daughter' populations, so it is necessary to control for the effects of phylogeny when testing adaptive hypotheses about these traits. Family organisation, kinship and pastoralism show a particularly strong association with population history. It is probable that in many cases traits are transmitted from parents to children within populations. Geographical diffusion appears to be less important in the transmission of most cultural traits, but is probably important for the transmission of the sexual division of labour and religion among populations.

1.5 Are humans adapted to the environments they inhabit today?

Maladaptation is expected to occur if environmental change is too rapid to be tracked by selection. It is widely believed among evolutionary psychologists (e.g. Cosmides et al., 1992) that there has not been sufficient time since the Pleistocene for humans to adapt to post-Pleistocene environments; it is hypothesised that humans remain essentially adapted to a foraging, stone age lifestyle. If this hypothesis were correct, then one would not expect the cultural diversity exhibited today to be adaptive. However, it is probably more realistic to expect a mosaic of partial adaptation and maladaptation among contemporary humans, as in other species (Irons, 1998; Strassmann and Dunbar, 1999). The amount of maladaptation arising from 'phylogenetic inertia' (Wilson, 1975) depends on two parameters, the rate of environmental change, and the rate of the selective response.

The efficiency of selection. Irons (1998) reviewed evidence for rapid evolutionary change (i.e. within a few thousand years) across many species. Many cases of rapid evolution by natural selection have been recorded, for example the evolution of five new species of cichlids in Lake Nabugabo in four thousand years. The degree of phylogenetic constraint is expected to vary among different traits. Across species, behavioural traits are generally considered to be evolutionarily labile (Gittleman et al., 1996), and behavioural lability might also be expected among humans. Cultural

behaviour is capable of much faster change than genetic behaviour, and can track a changing environment (Feldman and Laland, 1996; see above). Some adaptive genetic traits have also probably spread since the Pleistocene in modern humans. For example, since the domestication of cattle around 10,000 years ago, the gene for lactase persistence is thought to have increased from a frequency of less than 0.01 to a frequency around 0.7 in several populations which drink milk (Bodmer and Cavalli-Sforza, 1976; Aoki, 1986; Flatz, 1987). In contrast, a number of populations which adopted pastoralism more recently are still predominantly lactase non-persistent (e.g. the Herero, Currie et al., 1978; see chapter 4). It has also been hypothesised that high prevalence of sickle cell trait (a genetic trait) in West Africa is an adaptation to an increased prevalence of *falciparum* malaria, associated with the spread of slash-and-burn agriculture. Agriculture is hypothesised to have increased the breeding habitat (sunlit pools) of *Anopheles gambiae*, the main carrier of *Plasmodium falciparum* (Livingstone, 1958; Durham, 1991). These cases suggest that there has been enough time for genetic adaptations to agriculture and pastoralism to spread (c.f. Cosmides et al., 1992).

Environmental change since the Pleistocene. Many reproductive and productive trade-offs which people face in traditional agricultural societies today may be similar to the choices faced by hunter-gatherers in the past. Evolved psychological mechanisms or rules for making decisions may therefore result in adaptive behaviour, despite the change from hunting and gathering to agriculture (Borgerhoff Mulder, 1991; Irons, 1998; c.f. Cosmides et al., 1992). If this is true, one would expect behaviour in agricultural societies to be adaptive, a hypothesis that is testable by

measuring the fitness consequences of contemporary behaviour (e.g. Borgerhoff Mulder, 1991; Smith and Winterhalder, 1992; Mace, 1996; Betzig, 1997).

Industrialisation. We might expect that people in industrialised societies would exhibit the most maladaptation, because industrialisation and urbanisation represent a dramatic change in the human environment, to which there has been less time to adapt. Many cases of apparent maladaptation occur in developed countries (Strassmann and Dunbar, 1999). These include 'diseases of affluence' such as obesity, non-insulin dependent diabetes and cardiovascular disease (Neel, 1969), the high prevalence of reproductive cancers among women in developed countries (Strassmann and Dunbar, 1999) and possibly low fertility rates in post-demographic transition societies (e.g. Kaplan et al., 1995; Irons, 1998).

Maladaptation in industrial environments is unlikely to affect the analyses in this thesis. All adaptive hypotheses tested here related to non-industrial societies. There were few industrial populations in the samples used, because populations of European origin are under-represented in the main ethnographic database used (the *Ethnographic Atlas*, Murdock, 1967). In addition, many ethnographic sources date back several decades, before most modern development in many cases. Populations from industrialised countries were excluded from the sample entirely in the study of sexual dimorphism in stature (chapter 6), in order to remove the effects of the secular trend from the results (c.f. Tobias, 1985).

Migration and gene flow. Gene flow among populations, which has increased greatly in recent years (Cavalli-Sforza et al., 1991; Durham, 1991), can reduce local genetic

and cultural adaptations by introducing genes from populations under different selection pressures. For example, Wang et al. (1984) found that the frequency of lactase persistence was significantly lower in Mongols than in Kasakhs, both pastoralists in Northern China. They suggested this was because there has been extensive gene flow from the Han Chinese (non-pastoralists) into the Mongol population. Migration to a novel environment can also result in maladaptation. For example, white Australians experience high rates of skin cancer. To reduce the extent of maladaptation due to recent gene flow and admixture, only 'aboriginal' populations were studied in this thesis, defined as populations which inhabited approximately their present location in 1492. Recently admixed populations were also excluded, reducing the effect of recent migrations (Cavalli-Sforza et al., 1994).

1.6 Outline of chapters 2-7

In chapter 2 the validity of tree models of population history is discussed. Genetic and linguistic trees, used to provide information about population phylogeny, are described.

In chapter 3 the statistical methods used in this thesis are described. This includes two comparative methods, Felsenstein's method of comparative analysis using independent contrasts and Pagel's maximum likelihood method for detecting

correlated evolution in discrete traits on a phylogeny. The method used to investigate the transmission of traits among populations is described.

In chapters 4, 5 and 6 three cases studies are described, in which phylogenetic comparative methods were used to study cross-cultural variation. Adaptive hypotheses for variation in lactose digestion capacity in adults were tested in chapter 4. The socio-ecological correlates, and adaptive function, of matriliny and patriliny in Africa were investigated in chapter 5. Adaptive hypotheses for variation in sexual dimorphism in stature were tested in chapter 6. In each study the transmission of the traits tested among populations was also investigated.

The results of individual case studies are discussed in chapters 4, 5 and 6. The results of the investigation into the transmission of traits between populations are summarised in chapter 7, and some general issues in phylogenetic cross-cultural comparison are discussed.

Chapter 2

Tree models of human population history

2.0 Summary

Phylogenetic comparative methods were designed to test for evolutionary convergence across species. To use phylogenetic comparative methods at the population level (within a species), the species must be divided into distinct, partially isolated populations, and these populations must be related in a hierarchical, branching pattern, like species (Foster and Cameron, 1996). Do human populations fulfil these criteria? Tree models of human population history have been criticised, because there is gene flow and admixture between populations (e.g. Bateman et al., 1990; Moore, 1994; 1995; Dewar, 1995). In this chapter the following questions are asked. Can distinct, partially isolated populations be distinguished? Do cultural and linguistic barriers create partial boundaries between populations? How much gene flow and admixture is there between human populations? Do genetic and/or linguistic trees reflect population history? It is concluded that distinct, hierarchically related

human populations do exist, and that genetic and linguistic trees can be used as models of the past relationships between populations.

2.1 Sub-division among human populations

In this section I will discuss the distribution of human populations, focussing on the question of whether distinct, partially isolated human populations exist. This question is important in cross-cultural comparison: first, in defining the units for comparison, and second, in determining the proportion of variation expected to occur within, rather than between, populations. Knowing the rate of gene flow between populations is also necessary for interpreting genetic distance trees (section 2.2).

Can distinct populations be identified? Species with a large geographical range are usually sub-divided into smaller populations, meaning that reproduction is not random over the whole species range, but mostly occurs within smaller populations. Gene flow between populations is limited by distance, geographical barriers, and, in humans, linguistic and/or cultural differences (Cavalli-Sforza and Bodmer, 1971; Jorde, 1980; Gillespie, 1998).

In humans the major continental populations are morphologically distinct, to the extent that they would be called sub-species in another species (Cavalli-Sforza and

Bodmer, 1971; Mayr, 1963; Wright, 1978). But visible morphological differences (e.g. in skin colour) do not coincide with variation in gene frequencies in other traits (e.g. blood groups). Most morphological and genetic variation across geographical regions is gradual, not abrupt (Cavalli-Sforza et al., 1994). So is it appropriate to talk of 'populations' as opposed to genetic clines? The answer is 'yes' for two reasons. First, any comparative study implicitly recognises the presence of distinct populations in the sample, even if geographical variation is gradual. Second, cultural and linguistic boundaries exist between human populations, and most social interaction, including marriage and reproduction, occurs within local populations, although they are not completely isolated or discrete.

There is a high level of genetic similarity among populations – what does this imply about sub-division among populations? The larger proportion of genetic variation in humans occurs within local populations rather than between populations or continental 'races' (Lewontin, 1972; Nei and Roychoudhury, 1974; Latter, 1980; Barbujani et al., 1997). Lewontin (1972) measured genetic diversity in among populations. He found that 85.4% of genetic variation occurred within local populations, 8.3% between populations of the same race, and 6.3% between races. Latter (1980) and Barbujani et al. (1997) obtained similar results. The genetic similarity among populations indicates either that human populations have a recent origin, or that there has been a high rate of gene flow among populations, or both. These two possibilities are discussed further below. It is thought that modern populations have a relatively recent origin, and that the genetic similarity among populations arises mainly because of their recent origin, not because of high levels of gene flow (Cavalli-Sforza et al., 1994).

Defining populations for cross-cultural comparison. Populations can be characterised by gene frequencies, morphology, geography and cultural factors. Populations can be distinguished at different levels, from the local group (e.g. a single village) to large continental groups (often called 'major races'). At no level can entirely discrete or distinctive populations be distinguished. Language is probably the single most widely used marker of population boundaries by anthropologists. Language differences are probably an important force promoting isolation among human populations. In this thesis, most populations sampled were 'cultures' or 'anthropological populations'. An anthropological population is defined as a group of individuals sharing a common language and customs, identified by name. Ideally, for the purposes of phylogenetic comparative analysis, populations should also be geographically clustered and endogamous, with random internal mating, and there should be a one-to-one relationship between populations and languages.

Measuring sub-division among populations. The degree to which a species is sub-divided can be measured by comparing the observed number of heterozygotes within populations to the number of heterozygotes that would be expected under random mating across whole species. Sub-division increases the level of homozygosity above the level expected under random mating across the whole species, because the effect of drift is greater in small populations. Gene frequencies remain the same across the whole species, but the apportionment of genetic variance shifts from within populations to between populations (Wahland, 1928, quoted in Cavalli-Sforza et al., 1971). Sub-division can be measured using the fixation index, F_{ST}. F_{ST} is the probability that a locus is homozygous (or that two random gametes are identical)

within a population with random mating, relative to the probability that the locus would be homozygous if there were random mating across the whole species. It is calculated by:

$$F_{ST} = (H_T - H_S)/H_T$$

where H_T is expected heterozygosity a randomly mating species, and H_S is expected heterozygosity within a population in a sub-divided species. The expected level of heterozygosity at a two allele locus, in a population in a Hardy-Weinberg equilibrium (i.e. with random mating) is $2pq$, where p and q are the frequencies of the two alleles (Jorde, 1980; Hartl, 1988; Cavalli-Sforza et al., 1994). A goodness of fit chi-square statistic can be used to measure the degree of departure from Hardy Weinberg (random mating) within populations. Mating is closer to random in unstratified, local populations than in stratified populations, cities or larger regions (Jorde, 1980; Cavalli-Sforza et al., 1994). However, many 'anthropological' populations have significant internal sub-division, with genetic differentiation between sub-sections, which has the effect of reducing F_{ST} (Jorde, 1980).

F_{ST} can also be used as a measure of genetic distance between populations, used to construct genetic population trees. Discussing the impact of departures from Hardy Weinberg on F_{ST} genetic distance trees (see section 2.2.3), Cavalli-Sforza et al. (1994) stated that the consequences of departures from Hardy-Weinberg within local cultures are relatively minor, compared to genetic differences between more distantly related populations.

The fixation index F_{ST} has a theoretical range from 0 (no genetic divergence among sub-populations) to 1 (fixation). Wright (1978:85) suggested that F_{ST} in the range of 0-0.05 indicates little (but not necessarily negligible) genetic differentiation among populations and F_{ST} of 0.5-0.15 indicates moderate genetic differentiation. F_{ST} greater than 0.15 is not found among human populations (Cavalli-Sforza et al., 1994; Mountain, 1998; see below). Low F_{ST} may indicate either recent common ancestry among populations (i.e. a non-equilibrium state, where populations are in the process of diverging) or high rates of gene flow among populations in equilibrium (Felsenstein, 1982; Mountain, 1998). Results of empirical studies testing F_{ST} among human populations are described below.

F_{ST} can also be estimated using migration models, which measure the effects of gene flow on the random component of inbreeding in partially isolated populations. The parameters of migration models include the rate of migration (gene flow), the population size, and the spatial distribution of populations. Migration models include the island model (Wright, 1943), isolation by distance models (Wright 1943; 1946; 1951; also Malécot, reviewed in Cavalli-Sforza and Bodmer, 1971 and Jorde, 1980) and the stepping stone model (Kimura and Weiss, 1965).

To give an example of calculating F_{ST} using migration models, this calculation is described for the island model (the simplest model). In the island model (Wright, 1943), each population inhabits an 'island', receiving a proportion of its genes from other islands (the gene pool of the whole species) at each generation. In this model, if populations are in drift equilibrium, F_{ST} can be calculated from the population size and migration rate using the equation:

$$F_{ST} = 1/(4Nm + 1)$$

where N is the effective population size, and m is the migration rate (Cavalli-Sforza and Bodmer, 1971). In the island model, migration is equally probable from any other island, so gene flow is independent of distance. This makes the island model an unrealistic model of most natural populations. In isolation by distance models, the population is evenly distributed across space, and gene flow is a function of distance (Wright 1943; 1946; 1951; Jorde, 1980). In the stepping stone model, populations are clustered like villages or towns (Kimura and Weiss, 1965). Genetic differentiation occurs even though there are no barriers except distance between populations. Mathematics for calculating F_{ST} from the population size and migration rate in these models is described in Cavalli-Sforza and Bodmer (1971). Empirical studies of sub-division among populations using genetic or migration data are discussed below.

Rates of gene flow. Jorde (1980) reviewed studies of sub-division among local populations. There is moderate differentiation ($F_{ST} \cong 0.05$) between local anthropological populations in many regions, especially in South America, Australia, Papua New Guinea, the Island Pacific, Africa and less developed parts of India. Interpreting F_{ST} in terms of gene flow among populations requires knowledge of the date since divergence among the populations being compared. If the populations diverged relatively recently, then even moderate fixation may indicate a high level of local endogamy. Because the date to the common ancestor of populations inhabiting the same region is probably often recent, levels of F_{ST} around 0.05 indicate that local endogamy is high. Jorde (1980) found that F_{ST} tended to be highest among traditional

agricultural populations. F_{ST} tended to be lower in nomadic populations than in sedentary populations, probably because nomadic populations have higher mobility at marriage. F_{ST} is usually lower in developed regions than among subsistence populations. This is for two reasons. Developed regions have better communications, reducing local endogamy, and populations in modern states are more internally sub-divided than traditional anthropological populations, reducing F_{ST} (Jorde, 1980; Cavalli-Sforza et al., 1994). Jorde (1980) also reviewed studies which use Malécot's isolation by distance model. This gives a coefficient of local kinship a which is similar to F_{ST}. Most studies of hunter-gatherer and horticulturalist populations found that local kinship was high (mean a=0.038, n=24). Local kinship was lower in modern continental populations (Europe and Japan, mean a=0.005, n=21) and modern island populations (in Europe, mean a=0.008, n=22).

Gene flow can also be measured using migration matrices. The migration rate is estimated from the frequency distribution of the distance between the birthplaces of parents and children populations (Bodmer and Cavalli-Sforza, 1968; Hiorns et al., 1969). Because patterns of migration at marriage are usually different for men and women, this distance is usually calculated separately for mothers and fathers. Endogamy rates in rural Italy and historical Britain were found to be high (Cavalli-Sforza and Bodmer, 1971; Weiss, 1996).

Rates of gene flow across continents. Several studies have measured F_{ST} among the major populations worldwide. Wright (1978) compared seven populations worldwide, using classical genetic markers (blood groups and protein polymorphisms). He estimated $F_{ST} = 0.1248$. Cavalli-Sforza et al. (1994) compared 491 populations

worldwide using classical genetic markers. They estimated $F_{ST} = 0.119$. Mountain (1998) reviewed two worldwide studies which used RFLPs and STRs, which estimated $F_{ST} = 0.148$, and $F_{ST} = 0.139$ respectively. These results are consistent. Again, to interpret these results it is necessary to know the date of the origin of modern populations. The date of the most recent common ancestor of modern humans is estimated to be relatively recent (section 2.2), indicating that rates of gene flow among the major continental populations have probably been low.

Goldstein et al. (1995) developed a method of calculating absolute dates from genetic distances, using microsatellite variation. The genetic distances between populations can be compared to the known dates of separation of populations from archaeology. If the two dates are similar, this suggests that little gene flow among populations has taken place since separation. High rates of gene flow would be expected to retard genetic divergence among populations. The results of their study suggested that rates of gene flow among continental populations have been low.

The evolutionary consequences of sub-division: divergence among populations.

Genetic isolation causes divergence among populations, mainly through random drift (the random loss of alleles leading to the fixation of one allele in a population). The effect of drift is inversely related to population size, so that small, isolated populations are more prone to divergence through drift. Migration, or gene flow between populations, counteracts the effects of drift, causing convergence between populations.

Wright (1931) showed that the exchange of, on average, one individual per generation between two populations is sufficient to prevent the fixation of alleles through drift. This effect is independent of population size, for the following reason. A given number of immigrants (for example, one individual) represents a larger proportion of the total population size in a smaller population, so producing a larger effect of gene flow. But the effect of drift is inversely proportional to population size, so the effect of drift is larger in a smaller population. Gene flow and drift cancel one another out, and so the effect of immigration is dependent on the number of immigrants, independent of population size (Slatkin, 1987).

Over short time periods, mutation has less impact than drift and migration because the mutation rate is low (Cavalli-Sforza and Bodmer, 1971; Jorde, 1980). Over longer time periods, mutation and selection have an important effect on gene frequencies and genetic variation. Morphological variation among populations in different parts of the world, for example in skin colour, is probably the result of selection in different climates (Cavalli-Sforza and Cavalli-Sforza, 1995). Some polymorphic loci show large variation between populations, for example the Duffy locus (Latter, 1980) and lactose digestion capacity (chapter 4). These genes vary among populations because they have been strongly selected in some environments (Aoki, 1986; Flatz 1987, Feldman and Cavalli-Sforza, 1989). Wright (1943) showed that reproductive isolation in sub-divided populations permits the evolution of adaptation to local environments, resulting in divergence between populations. Gene flow can counteract the effect of selection, by introducing genes from a wider gene pool that is not under selection for the same adaptations. Wright (1943) also showed that isolation enables different

phenotypes, of similar but not identical fitness, to be established in different populations.

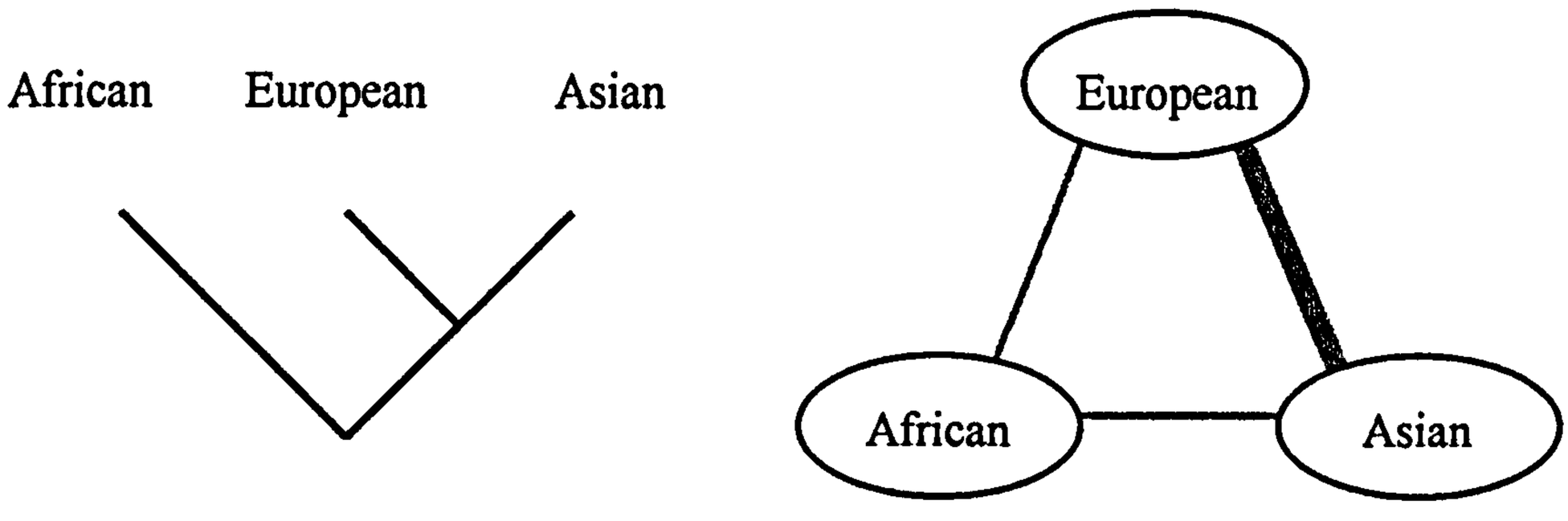
It is an interesting question how far cultural traits are subject to similar to processes of mutation, drift, selection and migration. Isolation among populations may promote cultural variation. The isolation of remote populations until recently enabled the survival of 'sub-optimal' cultural traits, for example, stone tool technology in Papua New Guinea. The loss of local cultural adaptations following contact between previously isolated cultures has been widely observed (e.g. Durham, 1991). 'Cultural drift' may also occur in isolated populations. Diamond (1998) describes the loss of cultural traits in isolated cultures, for example the loss of fishing technology, needles and other bone tools in Tasmania after 1500BC (p312-3). Japan virtually abandoned the use of guns after 1600, but reintroduced the manufacture of firearms within the country following contact with the U.S. Navy in 1853 (p257-8). The inheritance of cultural traits is not Mendelian, and so the effects of isolation would not be expected to be identical to genetic traits, but in some respects they may be similar.

2.2 Genetic trees and population history

Gene frequency trees reflect population history accurately if there is no selection, gene flow or admixture. Genetic divergence among populations is then a function of time, and gene frequency trees reflect actual demographic events (fission and divergence among populations). Branch lengths are proportional to time (the molecular clock) (Jorde, 1980; Cavalli-Sforza et al., 1994). But gene frequency trees can also reflect variable rates of gene flow, and differences in effective size among populations (Felsenstein, 1982; Mountain, 1998). In Figure 2.1 are shown, on the right, variable rates of gene flow between three stable populations, which could give rise to a genetic distance tree that is indistinguishable from a phylogenetic tree, shown on the left. The rate of gene flow, or the date of the most recent common ancestor of populations in the sample, needs to be known, to distinguish between these possibilities. If the rate of gene flow has been low, or if the date of the most recent common ancestor is recent, then genetic trees are more likely to reflect demographic history.

Figure 2.1 Interpreting genetic distance trees

On the left, a phylogenetic tree showing past relationships among three populations (in Africa, Europe and Asia) is shown. On the right are shown variable rates of gene flow (indicated by the thickness of the lines joining the populations) between three stable populations, which could give rise to the same tree. Modified from Felsenstein (1982) and Mountain (1998).



It was concluded in section 2.1 that rates of gene flow among populations in the past were relatively low. There is considerable evidence for a recent origin of modern humans, discussed below. Genetic population trees, it is concluded, do reflect population history, characterised by expansion and fission over the past 100,000 years (Cavalli-Sforza et al., 1994). However, some gene flow, admixture, variation in size, and selection does occur, and affects genetic trees. The effects of gene flow, admixture and variation in population size on genetic trees are discussed in this section. The effect of selection is discussed in section 2.2.3.

Dating the most recent common ancestor of modern humans. There are two competing models of modern human origins, the replacement ('Out of Africa') model, and the multi-regional model (Rethelford, 1995). According to the replacement model, all living humans share a recent common ancestor (probably African) dated to 1-200,000 years ago. This population expanded over the rest of the world with little or no genetic admixture with earlier humans. In the multi-regional model there was substantial gene flow among all humans (archaic and anatomically modern) throughout the past 1 million years (Harpending et al., 1993; Rethelford, 1995; Mountain, 1998). Under the multi-regional model, genetic trees would probably reflect patterns of gene flow among long-established populations (Felsenstein, 1982; Harpending, 1994).

Genetic evidence for the replacement model. Most genetic evidence tends to support the replacement model with a recent African origin of modern humans. The level of genetic diversity can be used to estimate the long term effective population size, and the date of divergence of individual genes. The origin of diversity in individual genes usually pre-dates population divergence, unless there has been gene flow (see below). The long-term effective population size of living humans, estimated using the mitochondrial coalescent, is thought to be around 10,000 individuals. Such a low population size is difficult to reconcile with a model of constant gene flow across the entire range of archaic *Homo sapiens* (Harpending et al., 1993; Harpending, 1994). On trees of individual genes, the origin of current diversity in mtDNA and Y-chromosome data has been dated at 50-500,000 years ago (studies reviewed in Mountain, 1998), and the MRCA of ß-globin data has been dated at 770,000 years ago (Harding et al., 1997). These dates are generally consistent with a recent common

ancestor of modern humans, although the date of 770,000 years ago from ß-globin may also be consistent with the multi-regional model. Using microsatellite data, and a measure of genetic distance that is independent of population size, Goldstein et al. (1995) estimated the date of divergence between African and non-African populations to be 115,000 years, with 95% confidence intervals of 75,000-287,000 years. This result tends to support the replacement model, but these confidence intervals did not take account of uncertainty in the mutation rate, so they should probably be wider.

The effect of gene flow on a genetic tree. The effect of gene flow on genetic population trees is to shorten the branch lengths, so that the time since the divergence of populations will be under-estimated from genetic distances (Weiss, 1996). If gene flow is homogenous across the tree, branch lengths will retain the same proportions within the tree. If the amount of gene flow is variable across the tree, parts of the tree with high gene flow will appear younger relative to parts of the tree with low gene flow. On a gene tree (i.e. of a single gene, not populations), if an allele passes between populations by gene flow, the time to coalescence for that allele will post-date population divergence (Mountain, 1998).

Admixture. Admixture is merging between previously divergent populations. The contribution of two parent populations, A and B, to an admixed population M, can be estimated from gene frequencies in the three populations using the equation:

$$q_M = (1 - m)\, q_B + m q_A$$

(taken from Cavalli-Sforza et al., 1994, equation 1.17.1) where q is a given gene, so q_A and q_B are the frequencies of that gene in the two ancestral populations, and q_M is the frequency of that gene in the admixed populations. The proportion of the admixed gene pool contributed by population A is m and the proportion contributed by population B is $(1 - m)$. If there is a small proportion of gene flow into a population over many generations, the gene pool of the receiving population is eventually entirely replaced (Cavalli-Sforza and Bodmer, 1971; Hartl, 1988; Cavalli-Sforza et al., 1994).

The effect of admixture on genetic distances is to shorten the distance between the admixed population and its parental populations. This can be detected in a distance matrix by testing whether any distances are unexpectedly short (under a hypothesis of equal evolutionary rates, all populations descended from the same ancestor are expected to be equally distant from one another) (Cavalli-Sforza et al., 1994).

Admixture among populations requires a network model rather than a tree (using the term 'network' to mean a tree with anastomoses, not to mean an unrooted tree). Genetic network models are beginning to be developed (e.g. Brandelt et al., 1995) but available phylogenetic comparative methods only use trees, not networks. Admixed populations included on trees are joined as outliers to the parental branch that contributed most to their ancestry (Cavalli-Sforza et al., 1994). This is probably seen on the genetic trees of Cavalli-Sforza et al (1994), for example in the Lapps who are joined to the European branch as an outlier (see Figures 4.2 and 4.3, chapter 4). The

Lapps are believed to be an admixed population of Uralic-Asian and European ancestry.

Population size. Differences in size among populations can also affect genetic trees. Extended bottlenecks (small population size) increase genetic divergence between populations because of increased drift in small populations. The time since population divergence is then over-estimated from branch lengths (Livshits and Nei, 1990).

Were gene flow and admixture rarer in the past than today? Where estimates of local endogamy are available across time periods, they usually show a decline in genetic isolation towards the present (Jorde, 1980). Contact between populations is increasing all the time, with increased gene flow and genetic convergence among populations. In the past, populations probably experienced greater isolation, especially across long distances (Durham, 1991; Cavalli-Sforza et al., 1994). If most admixture is a modern phenomenon, it is possible to reduce its effects by excluding recently admixed populations from the dataset. This was done in this thesis, following Cavalli-Sforza et al. (1994), who aimed to sample the extent of genetic divergence among populations before the increase in inter-continental travel in modern times. Cavalli-Sforza et al. sampled populations which inhabited approximately their present location before 1492, and excluded 'admixed' populations, for example Native American populations with more than 10% admixture with Europeans.

2.2.1 Tree models and cultural history: ethnographic criticism of tree models

Moore (1994) disputed the claim that that most population admixture is recent, arguing that gene flow and admixture occurred throughout prehistory, and that population history therefore cannot be represented using trees. He used ethnographic evidence from Plains Native Americans to argue that cultures were fluid, prone to merging, and that individuals passed between cultural groups regularly. Several other issues are raised in Moore's criticism of tree models of cultural phylogeny. How far are cultural groups continuous through time? How far do cultural units correlate with biological populations (i.e. groups of individuals within which most reproduction occurs)?

Cultural continuity through time. Continuity in cultures through time is an ongoing area of research in anthropology. For example, Vail (1989) has investigated the extent to which southern African cultural groups were formed during the colonial period, and how far they descend from indigenous groups that existed before the colonial era. In social anthropology, the main focus of this research is the historical development of ethnic identities, rather than the persistence of populations in the biological sense. However this literature (historical ethnography) could also be examined to see how far genetic population trees correlate with historical evidence about the history of populations. Evolutionary tree models can incorporate some types of cultural change

through time, including evolutionary change within cultures, and fission (although not fusion) of cultures (chapter 3).

How far do cultures correlate with biological populations? A *belief* in common descent is a defining aspect of ethnic identity (Smith, 1986) but not all members of a culture necessarily actually descend from the recognised ancestors of that group. Individuals can pass across cultural boundaries, becoming members of a different cultural group to the one they were born into (Barth, 1969). However, migration between cultures is relatively uncommon, and most individuals marry within the cultural group into which they were born. Cultural practices are passed on to their children, so the cultural unit and the biological population are usually perpetuated simultaneously (e.g. Smith, 1986).

More work remains to be done on cultural continuity through time and the extent of merging among cultures, especially to integrate qualitative ethnographic studies with mathematical approaches from population genetics. Some critiques of tree models of cultural phylogeny (e.g. Moore, 1994; 1995) suggest that gene flow makes tree models of population history invalid. This is probably too pessimistic. Migration models (see above) show that genetic divergence will occur if gene flow is limited or local. Gene flow from neighbouring cultures has less impact than long-distance gene flow because neighbouring cultures tend to be genetically similar. Trees may be good models of past relationships among distantly related populations, even if there is gene flow among more local populations (Cavalli-Sforza et al., 1994).

2.2.2 Summary: do genetic trees reflect population history?

Demographic history over the past 100,000 years has been characterised by population expansion, first with a population expansion out of Africa, and then with recent population expansions, coinciding with technological advances such as agriculture and military technology (Cavalli-Sforza et al., 1994). Genetic trees showing relationships among populations (e.g. Cavalli-Sforza et al., 1988; 1994; Nei and Roychoudhury, 1993) probably reflect actual population events of fission and divergence throughout this population expansion, rather than variable rates of gene flow among populations. This interpretation of genetic trees is supported by evidence for a recent common ancestor of modern humans (Goldstein et al., 1995; Mountain, 1998); small long-term effective population size, supporting the 'replacement' model of modern human origins (Harpending et al., 1993; Harpending, 1994); low rates of gene flow across continents (Goldstein et al., 1995); and a correlation between relative branch lengths and archaeological dates of colonisation of the major continents (Cavalli-Sforza et al., 1988; 1994; Nei and Roychoudhury, 1993; Goldstein et al., 1995).

2.2.3 Worldwide genetic trees

Gene frequency trees were used as models of population history in this thesis (chapters 4, 5 and 6). Most of the trees used were Cavalli-Sforza et al.'s (1994) F_{ST} genetic distance trees. Cavalli-Sforza et al.'s trees are described, and compared to other published genetic population trees, in this section.

Genetic distance trees using classical markers. Cavalli-Sforza et al. (1994) constructed genetic distance trees from gene frequencies of classical genetic markers (blood groups and protein polymorphisms). The major advantage of classical genetic markers is that many populations worldwide have been tested for these markers. A disadvantage is that classical markers are expressed characters, so may not be selectively neutral. Selection (stabilising or disruptive) means that the distance between populations will not be a function of the time since their divergence. However, Cavalli-Sforza et al.'s trees were not thought to be strongly affected by selection. Cavalli-Sforza et al. tested the assumption of neutrality in the markers they used, by comparing the observed with the expected genetic distances between populations. A small number of loci in the dataset were found to have smaller or larger than expected differences among populations, indicating that they may be under stabilising or disruptive selection. Genes linked with protection against *falciparum* malaria were excluded from the dataset before the trees were constructed. It has been found that trees constructed from a large number of classical markers are similar to trees made from DNA sequence data and microsatellites, suggesting that

classical markers do reflect population history, despite the effects of selection (Bowcock et al., 1994; Mountain, 1998).

F_{ST} distances. Cavalli-Sforza et al. (1994) used a genetic distance statistic *d* to weight genes with different frequencies. The statistic *d* is equivalent to F_{ST} when two populations are being compared, and can be calculated by:

$$d = F_{ST} = V_p / p(1-p) \quad \text{[Cavalli-Sforza et al., 1994: section 1.11.2]}$$

where V_p is the variance in gene frequencies and *p* is the mean gene frequency. In a set of *n* populations, F_{ST} is equal to the average of all the possible pair-wise values of *d*. To estimate the genetic distance between populations, Cavalli-Sforza et al. (1994) use a genetic distance measure *D*, a function of *d* which is proportional to time:

$$D = \log(1 - F_{ST}) = t / 2N \quad \text{[Cavalli-Sforza et al., 1994: section 1.11.2].}$$

In this equation log is the natural logarithm, *t* is the time since separation and N is the effective population size. *D* is equal to *t* / 2N under a model of divergence through drift when F_{ST} is small, as is the case among human populations. Cavalli-Sforza et al. (1994) refer to genetic trees constructed using the genetic distance *D* as F_{ST} trees, because *D* is a function of F_{ST}.

Tree building. Cavalli-Sforza et al. (1994) used average linkage to construct trees from their genetic distance matrices. Average linkage, or UPGMA (Unweighted Pair-Group Method using arithmetic Averages) is a method which first groups together the

two closest populations in a matrix (to form the lowest clade on the tree), then pools them, decreasing the matrix size by one, then repeats the process. They used this method because it was simple but performed well (making few errors) in simulations. Average linkage is based on a model of constant evolution across the tree, an assumption which received partial support from a comparison of genetic distances with the dates of earliest colonisation of continents from archaeology (Cavalli-Sforza et al., 1988).

Worldwide genetic distance trees. The deepest split on most genetic trees inferred from nuclear DNA is between Africans and other populations (e.g. Nei and Roychoudhury, 1993; Cavalli-Sforza et al., 1994; Bowcock et al., 1994; Mountain, 1998). This indicates either that the sub-Saharan African population has been the most isolated population, or that it is the oldest population, or that it had a larger long term size, perhaps having undergone a population expansion earlier (Harding et al., 1997). It has been suggested that the Sahara desert may have been an isolating mechanism, although the degree of aridity in the Sahara has varied across time (e.g. Bower, 1995). It seems probable that both greater age (as in the replacement model) and larger long term effective population size underlie the position of Africa in genetic trees (Harding, 1997; Mountain, 1998). There is less consensus among trees about the co-ordinates of the other continental populations. The position of the Eskimos also varies on different trees.

On Cavalli-Sforza et al. (1994)'s F_{ST} tree, the second highest split was between Australians and New Guineans (who clustered together) and other non-African populations. Native Americans, east Asians and Caucasians formed a clade

('Caucasian' refers to Europeans, South Asians, North Africans and populations from the Middle East). Eskimos clustered with north Asians, not with other Native Americans. Southeast Asians and Pacific Islanders clustered together. Cavalli-Sforza et al. (1988) constructed another tree from the same 42 populations using a different measure of genetic distance (developed by Nei). On this tree, Southeast Asians clustered with Australians and New Guineans in the second split on the tree. In other respects, this tree is very similar to the F_{ST} tree of Cavalli-Sforza et al. (1994).

Nei and Roychoudhury's (1993) worldwide genetic tree of 26 populations was constructed using a neighbour-joining (NJ) method of tree building, developed by Nei. Unlike average linkage, NJ allows different parts of the tree to have different evolutionary rates. This is probably more realistic because population size affects the rate of divergence among populations (Livshits and Nei 1990). On this tree, the second split was between Caucasians and all other non-Africans. Native Americans and Eskimos formed a clade in contrast to Cavalli-Sforza et al.'s (1988; 1994) trees. Using microsatellite polymorphisms, Bowcock et al. (1994) constructed a tree of the major continental populations. On this tree, the second split was between Europeans and other non-Africans, as on Nei and Roychoudhury's (1993) tree. East Asians and Native Americans formed a clade, as on Cavalli-Sforza et al's (1988; 1994) trees. Pacific Islanders, Australians and New Guineans formed a clade.

There is a fairly high level of consistency across trees in the populations which tend to cluster together within continents (with the exception of Eskimos). For example, Pacific Islanders consistently cluster together, despite conflict among trees about their relationships to other populations. This increases one's confidence in using genetic

trees for the purposes of phylogenetic comparative analysis. In phylogenetic comparative analysis, each node on a tree contributes one data point. Higher nodes (towards the root) and lower nodes (towards the tips) have equal weight (chapter 3).

In this thesis, each comparative analysis was repeated using more than one tree. Despite our uncertainty about which tree is the best model of the past relationships among populations, if the same result is obtained from several different trees, we can have more confidence that the effect found is real.

2.3 Language trees and population history

Like neutral genetic variation, linguistic differences in separated populations accumulate approximately as a function of time, so relationships among languages can reflect population history. The same ecological and demographic processes cause linguistic and genetic divergence among populations, so linguistic and genetic distances tend to be correlated. Ecological and sociological factors underlying linguistic divergence are discussed below. In section 2.3.1, evidence for a correlation between linguistic and genetic trees is reviewed. In section 2.3.2, methods of constructing language trees are discussed. The language trees used in this thesis are discussed in section 2.3.3.

Linguistic divergence among sub-divided populations. Language boundaries are defined by the criterion of mutual intelligibility among speakers. A linguistic speech community is the largest group of individuals who understand one another's speech. When a speech community becomes divided by distance or geographical or political barriers, linguistic changes accumulate within the separated speech communities. Initially this results in the evolution of regional dialects, eventually leading to the break-up of the language into divergent daughter languages (Trask, 1996).

There are many parallels between language change and biological evolution, noted by Darwin (1874):

> The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel (Darwin, 1874).

Speech communities can be compared to species: they are groups of individuals who, respectively, can communicate through speech or reproduce sexually (Mayr, 1963). Ecological and geo-political factors that separate populations result in simultaneous gradual divergence in language and genetic structure.

Like the genealogy of biological taxa, descent relationships among languages are frequently represented using trees. As in population genetics, there is debate about the validity of tree models of linguistic relationships, because tree models do not incorporate linguistic 'borrowing' between neighbouring speech communities. For example, Dewar (1995) studied Malagasy dialects, and found a strong geographical

pattern in the pattern of differences between dialects. He concluded that geographical proximity to neighbouring populations, not history, explains patterns of linguistic divergence on Madagascar (c.f. Felsenstein, 1982; Figure 2.1). However, his analysis did not control for the correlation that probably exists between historical relationship and geographical proximity; a geographical pattern can arise from patterns of descent among populations, because 'daughter' populations will tend to live near their ancestors (c.f. Harvey and Pagel, 1991; chapters 3-6).

2.3.1 Correlation between linguistic and genetic trees

Language trees and genetic trees are often similar because they reflect the same population history (Cavalli-Sforza et al., 1988; Ruhlen, 1991; Cavalli-Sforza et al., 1992; Penny, 1993).

Worldwide correlation between linguistic and genetic distances. Cavalli-Sforza et al. (1988) superimposed language phyla on a genetic tree of 42 populations worldwide. There was a high level of similarity between language phyla and genetic groups. Cavalli-Sforza et al. (1988) suggested that this was because linguistic and genetic divergence occurs simultaneously among populations. By implication, language trees contain information about population history. This paper was criticised by Bateman et al. (1990) for lacking a formal statistical test of the correlation between the genetic tree and the language tree. However, subsequently developed statistical tests for

similarity among trees show a highly significant similarity between the two trees (Cavalli-Sforza et al., 1992; Penny et al., 1993).

Correlation between linguistic and genetic distances within geographical regions.

Barbujani (1991) and Cavalli-Sforza et al. (1992) performed a meta-analysis of seventeen regional studies which tested for similarity between linguistic and genetic distances among populations from all continents. Seven out of seventeen studies reviewed showed a significant correlation between genetic and linguistic distance, a highly significant result because less than one study out of a sample of seventeen would be expected to be significant at the 0.05 level by chance. Barbujani and Sokal (1990) found that many linguistic boundaries in Europe corresponded to marked genetic gradients, suggesting either that populations from different language groups have different origins, or that language barriers act as a barrier to marriage, or both.

A number of other studies failed to find a correlation between genetic and linguistic distances. Black et al. (1983) found that linguistic similarity among populations in the Lower Amazon failed to predict genetic distances (using classical markers). Ward et al. (1993) measured genetic distance among three cultures in northwest coast America, the Haida (Na-Dene), the Bella Coola (Amerind, Salishan) and Nuu-Chah-Nulth (Amerind, Wakashan) using mtDNA. The Amerind cultures did not form a clade, as would be predicted if genetic and linguistic distances were correlated (assuming Amerind is a valid language phylum, see Table 2.4). However, the time to coalescence among the Haida was less than among the Amerind populations. This correlates with linguistic evidence that Na-Dene is younger than Amerind (see section 2.3.4). Moral et al. (1994) found that the Catalan-speaking population of northwest

Sardinia was genetically closer to other Sardinians than to Catalonians (see below). Sajantila et al. (1995) found that European populations from three language phyla (Indo-Hittite, Uralic-Yukaghir and Basque) were very similar in their mtDNA.

Language trees and genetic trees may differ for a number of reasons:

1. Rates of linguistic and genetic evolution may be different
2. Languages can spread without population replacement
3. Gene flow can occur without language replacement.

Rates of linguistic and genetic evolution. In the 19th century, Lyell (1863) hypothesised that languages and 'races' evolve at different rates:

> There can be no question that if we could trace back any set of cognate languages now existing to some common point of departure, they would converge and meet sooner in some era of the past than would existing races of mankind; in other words, races change much more slowly than languages (Lyell, 1863).

Sajantila et al. (1995), failing to find any differences in mtDNA among linguistically divergent European populations, suggested that mtDNA lineages arose before linguistic phyla. They suggested that nDNA may be preferable when testing for a correlation between linguistic and genetic distances, because nDNA frequencies may change on a timescale similar to linguistic evolution. Bateman et al. (1990) argue that language phyla are shallower than higher nodes on worldwide genetic trees. This is seen in the language trees used in this thesis (chapters 4-6) in which higher nodes are not resolved.

Language replacement. Language replacement can occur without a change in the genetic makeup of the population. 'Elite dominance' is when an invading political elite imposes its language on the local population (Renfrew, 1992). The idea of elite dominance can also be traced back to Lyell (1863). To explain how Indo-European languages came to be spoken by what he considered to be several distinct races in Europe and Asia, he hypothesised that Indo-European languages were imposed on pre-existing populations by a relatively small group of 'Aryan' warriors from north-west India:

> These conquerors may have been few in number when compared to the populations which they subdued. In such cases the new settlers, although reckoned by tens of thousands, might merge in a few centuries into the millions of subjects which they ruled...yet many of the words, and what is more to the point, some of the grammatical forms of their language, might be retained by the masses which they had governed for centuries, these masses continuing to preserve the same features which had distinguished them long before the Aryan invasions (Lyell, 1863).

Another example is the Sardinian city of Alghero, where the population has spoken Catalan since the 13th century, when it was conquered by the kingdom of Aragon. Alghero is genetically similar to the rest Sardinia, suggesting that there was little gene flow from Catalonia despite the language replacement (Moral et al., 1994).

Cavalli-Sforza et al. (1988) argued that language replacement of this type is mainly a feature of the last 5,000 years, associated with the rise of states and sophisticated military technology, and that it has not erased the earlier parallel evolution in languages and gene pools in most regions. Nichols (1997) disagrees, suggesting that languages in 'spread zones' (continental plains prone to foreign invasion, e.g. central Europe) have been replaced many times. She argues that only 'residual zones'

(peripheral mountainous regions, e.g. the Papua New Guinea Highlands) retain their aboriginal languages over millennia. If foreign invaders replace the local population, congruence between genetic and linguistic affiliation will be retained.

Gene flow without language replacement. Gene flow without language replacement is also possible. This can result in genetic convergence among populations belonging to different linguistic groups. Cavalli-Sforza et al. (1994: Table 1.17.1) show that with 5% incoming gene flow per generation, the gene pool of a population will be entirely replaced after 2,000 years (80 generations). McCall (1998) suggests that this may have occurred in Chadic speakers, who cluster genetically with sub-Saharan Africans but who are linguistically part of the predominantly North African Afro-Asiatic language phylum.

Correlation between language and other cultural traits. Welsch et al. (1992) tested for a correlation between language and material culture in northern New Guinea. They compared matrices of similarity in material artefacts with linguistic and geographical distances between populations, and found that geographical distance predicted similarity in material culture but linguistic similarity did not. They concluded that material artefacts were mainly transmitted by horizontal diffusion between neighbouring populations in this region (see chapter 1). An implication of this study is that language is not a marker of other aspects of cultural descent among these populations. However, Welsch et al.'s data were reanalysed by Moore and Romney (1994), who found that language and geography predicted patterns of material culture equally well in the sample, raising doubts about Welsch et al's original conclusions.

In summary, genetic and linguistic distances tend to be correlated, although the correlation is not perfect. Similarity in linguistic and genetic trees results from simultaneous genetic and linguistic divergence in sub-divided populations. Language trees can therefore be used as models of population history in phylogenetic comparative analysis (chapter 3).

2.3.2 Methods for constructing language trees

Language trees are constructed by identifying linguistic elements which are similar by descent across three or more languages. Form-function similarity across languages can result from common descent, borrowing and chance. There are also a small number of onomatopoeias like 'splash' and natural baby words like 'mama' which are common to many languages worldwide. Form-function similarities due to processes other than common descent need to be excluded before common descent can be established to be the cause of similarity among languages.

Borrowing. Borrowing is the diffusion of words or other linguistic elements across languages, equivalent to gene flow. Sometimes borrowing results in convergence among several languages to form a convergent linguistic area or *Sprachsbund* (Nichols, 1997). Tree diagrams do not show the extent of borrowing or convergence, only the genealogical origin of languages (Embleton, 1991; Trask, 1996). Borrowing

can usually be identified because it introduces irregular words into a language, and also affects specific areas of vocabulary (non-basic words) and geographically neighbouring languages (Ruhlen, 1994).

Constructing language trees. There are two distinct processes in the formation of language trees, a) identifying language phyla (the largest group of related languages), and b) identifying relationships among languages within phyla. The second process is the main work of comparative linguistics. The first process, recognising language phyla, arouses more controversy, especially for distantly related languages.

Identifying language phyla. Language phyla are the largest group of languages recognised to be related. Language phyla are identified by the presence of form-function similarities across languages at a higher rate than expected by chance (Nichols, 1997). A number of significance tests have been developed to test whether languages hypothesised to be related are more similar than expected by chance. Nichols (1996; 1997) described a method for estimating the probability of form-function similarity among words, in order to identify probable descent markers (sets of words more similar than expected by chance). Oswalt (1991) described a method of testing for higher than expected form-function similarity among languages, which controls for the average amount of phonetic similarity in the languages being tested.

Multilateral comparison. Greenberg (1963; 1987) developed a method for comparing multiple languages simultaneously (mass or multilateral comparison). The statistical power of multilateral comparison is greater than tests of relationship among pairs of

languages only (e.g. Oswalt, 1991). Ruhlen (1994) used the following example to demonstrate the statistical power of multilateral comparison. If a set of languages has 7 consonants (C) and 3 vowels (V), then 147 CVC words are possible. The probability that two languages assign the same meaning to a CVC root independently is 1/147 or 0.007. If more languages are included in the comparison this probability is reduced. The probability that multiple languages attach the same meaning to a CVC root is 0.007^{n-1}, where n is the number of languages in the sample in which that root has the same meaning. Most languages have more than 7 consonants and 3 vowels, reducing further the probability that form-function similarities arise by chance. It was assumed in this calculation (unrealistically) that each CVC root has an equal probability of occurring. Notably also most proposed etymologies in long-distance comparisons are not phonetically or semantically identical, increasing their probability.

Ringe (1996) argued that phonemes, not whole words or roots, are the appropriate unit for comparison in historical linguistics, because only phonemes are inherited in a regular way, exhibiting regular sound changes in languages through time. Among unrelated languages the frequency distribution of languages which attach the same meaning to a particular phoneme is approximately binomial, where p is the frequency of the phoneme estimated across the set of languages (using the Swadesh standard word list) (Swadesh, 1971b, see below). The probability of the same meaning being associated with a particular phoneme in a given number of languages in the sample, if the languages are *not* related, is shown in the binomial distribution. This is:

$$[n!/\, r!(n-r)!]\, p^r\, (1-p)^{n-r}$$

where *p* is the frequency of the phoneme across the set of languages, *n* is the set of languages and *r* is the number of languages where the phoneme has a particular meaning (Norton, 1982).

This method of estimating the probability of form-function similarities across languages provides a way of testing the significance of the results of multilateral comparisons. Ringe (1996) used this method to test the statistical significance of Greenberg's (1987) proposed Amerind etymologies (Table 2.1). He found no statistical support for the Amerind phylum.

Descent relationships within language phyla. Within language phyla, lower level (i.e. more closely related) descent groups are identified by the presence of shared linguistic innovations, equivalent to shared derived characters in biology (Ruhlen, 1991). Phonetic change within a language group is usually regular. The rules underlying phonetic change can be inferred from studying cognate words within that group. Ancestral languages are reconstructed following the rules of phonetic change. The recognition of cognate words is an iterative process. From an initial list of words hypothesised to be cognate, rules of phonetic change are inferred. The list of cognates is then modified from the inferred rules of regular sound changes (e.g. Grace, 1996).

Estimating branch lengths using glottochronology. Swadesh (1971b) developed a method of estimating branch lengths on language trees, based on a model of language change in which the proportion of cognates in related languages declines at a constant rate with time. This method is known as glottochronology, and is based on a model of linguistic change similar to the model of a genetic clock. The percentage of core

vocabulary shared by two related languages is used to estimate the time since their divergence. Swadesh compiled two standard lists of basic vocabulary, which is relatively resistant to borrowing, consisting of one hundred and two hundred words (Swadesh, 1971b; Trask, 1996). These word lists are used to compare the proportion of cognates among languages.

Swadesh (1971a: 284) estimated the relationship between time and linguistic divergence to be:

$$t = (2 \log r) / \log c$$

where t is time, c is the proportion of cognates in two languages today, and r is the proportion of ancestral words retained by any given language after 1,000 years. Further details on the mathematics are found in Embleton (1991). The retention rate r was calibrated from language change in written languages (e.g. Latin and Spanish). For the Swadesh 100-word list r is estimated to be approximately 0.86, i.e. 86% of vocabulary is conserved after 1,000 years, with a range from 81% to 90% (Swadesh, 1971b; Trask, 1996; Embleton, 1991).

The main weakness of this method is that is does not incorporate the effects of borrowing. Swadesh's standard word lists are relatively immune to borrowing, but borrowing does affect basic vocabulary to some degree. Moreover, the amount of borrowing varies among languages. The method produces highly inaccurate divergence dates for languages with more or less borrowing than average (Embleton, 1991). A method which takes into account the number of neighbours, and the rate of

borrowing from each neighbour, was developed by Embleton (1991) (the full equation is not reproduced here). Embleton's (1991) method performed well in computer simulations and for groups of languages whose dates of divergence are known from historical sources (e.g. Germanic). Embleton's method does not rely on Swadesh word lists. It can be used with any measure of linguistic similarity (not necessarily vocabulary).

Potentially, glottochronology could be used to assign branch lengths to language trees. But as yet this method has apparently not been widely implemented. The language trees used in this thesis (the main source is Ruhlen, 1991) had equal branch lengths. This is regrettable, because dated nodes on language trees could be useful for reconstructing cultural history (chapter 3).

2.3.3 Worldwide language trees

In this section (2.3.3) I will attempt to assess the status of the language phyla in Ruhlen (1991), a comprehensive source of data on language classification, used in this thesis.

The language classifications of Ruhlen (1987) provide the most comprehensive classification of languages available. Ruhlen used many sources, notably the language classifications of Greenberg (1963; 1971; 1987). Some of the language phyla

recognised by Ruhlen (1987) are generally accepted among linguists (e.g. Indo-European/Indo-Hittite) while others are not (e.g. Amerind). Controversial language phyla are often very old (>10,000 years) so time has obscured many similarities among languages. In Table 2.1 the language phyla recognised by Ruhlen (1987) are listed, with their geographical locations and a brief assessment of their general acceptability among historical linguists.

A number of higher-level language groups have been proposed, for example Nostratic which includes Indo-Hittite, Uralic-Yukaghir, Altaic, Afroasiatic, Kartvelian and Elamo-Dravidian. A macro-phylum proposed by Greenberg, called Eurasiatic, includes Indo-Hittite, Uralic-Yukaghir, Altaic, Chukchi-Kamchatkan and Eskimo-Aleut (Ruhlen, 1991). These macro-phyla are highly controversial, and were not used in this thesis.

The age of language phyla in Ruhlen (1987) is variable. Indo-Hittite is estimated to be ca. 6,000 years old. Afro-Asiatic is estimated to be ca.10,000 years old (Trask, 1996). I do not have age estimates for other phyla, although more controversial phyla (see Table 2.4) are generally older. The genetic clock or time to coalescence can sometimes be used to estimate the age of linguistic groups. For example, Ward et al. (1993) found that the Haida (a Na-Dene group) had less diversity in mtDNA than the Bella Coola and the Nuu-Chah-Nulth (Amerind groups, Salishan and Wakashan respectively), suggesting that the Haida are a younger population. The estimated time to coalescence in the Haida was 6,500 years, compared to 13,000 years in the Bella Coola and the Nuu-Chah-Nulth. This is consistent with the likely relative ages of Na-Dene and Amerind.

Table 2.1 Language phyla in Ruhlen (1987)

Phylum	Where spoken (pre-1492)	Comments
Afroasiatic	N. Africa, Middle East	Usually accepted (Trask, 1996). Recognised by Greenberg (1963). Nichols (1997) classifies Afroasiatic as a quasi-stock, meaning a probable ancient descent group, but one which is too old to be proven.
Altaic	Asia	Partly accepted. Turkic, Mongolian and Tungus generally accepted (Trask, 1996). No consensus on membership of Japanese, Korean and Ainu. Ruhlen (1987) includes these languages in Altaic but Ruhlen (1991) excludes them.
Amerind	North and South America	Highly controversial (Ruhlen, 1991; Trask, 1996). Recognised by Greenberg (1987). Nichols (1997) considers this group of languages to consist of 150 separate stocks. She recognises some common features among some languages in this pool (e.g. *m:n* pronouns across a wide area) but considers that they may have arisen by diffusion, or may be a universal language feature. Ruhlen (1994) shows that *m:n* pronouns are not a universal feature of language, but are unique to the Americas. Ringe (1996) tested the probability of Greenberg's (1987) proposed Amerind etymologies (excluding pronouns) and found that they were not more similar than would be expected by chance (section 2.3.2).
Australian	Australia	Controversial. Consists of Pama-Nyungan and non-Pama-Nyungan languages. Pama-Nyungan is accepted as a valid genetic group. The affiliations of non-Pama-Nyungan languages are more controversial, but may be related to Pama-Nyungan languages (Nichols, 1997; Ruhlen, 1991; Trask, 1996).
Austric	China and S.E. Asia	Controversial. Austric is a super-phylum, consisting of three generally accepted phyla, Miao-Yao, Astroasiatic and Daic (Ruhlen, 1991).
Austronesian	S.E. Asia, Pacific, Madagascar.	Accepted (Blench and Spriggs, 1997; Trask, 1996). Includes Malayo-Polynesian and some Melanesian languages.
Caucasian	Caucasus	Not generally accepted. Ruhlen (1991: postscript) splits this phylum into North Caucasian and Kartvelian
Chukchi-Kamchatkan	North Asia	Accepted (Blench and Spriggs, 1997; Trask, 1996)
Elamo-Dravidian	South Asia	Accepted (Blench and Spriggs, 1997; Trask, 1996)

Table 2.1 (cont.) Language phyla in Ruhlen (1987)

Phylum	Where spoken (pre-1492)	Comments
Eskimo-Aleut	Far North - America, Asia, and Greenland	Accepted (Ruhlen, 1991).
Indo-Hittite	Europe, Asia	Accepted (Nichols, 1997; Ruhlen, 1991)
Indo-Pacific	Papua New Guinea, Pacific Islands	Controversial. Recognised by Greenberg (1971). Nichols (1997) considers this phylum to consist of 80 independent stocks and isolates. Most languages of Papua New Guinea are considered to be a valid genetic group (Trans-New-Guinea) by Wurm (1982). He recognises 10 other phyla in 'Indo-Pacific', among which there is widespread ancient borrowing.
Khoisan	South and East Africa	Sometimes accepted (Ruhlen, 1994; Trask, 1996). Recognised by Greenberg (1963). Nichols (1997) considers click languages to be a structural pool, meaning a group of languages with some similarities, but whose similarities do not reach a threshold of statistical significance. She considers that the similarities among these languages may be due to ancient borrowing or genetic relationship, but that the connection between these languages is too remote to distinguish between these two possibilities.
Na-Dene	N. America	Usually accepted (Ruhlen, 1991; Trask, 1996).
Niger-Kordofanian	Central/South Africa	Generally accepted (Trask, 1996). Recognised by Greenberg (1963). Nichols (1997) classifies Niger-Kordofanian as a quasi-stock.
Nilo-Saharan	East and Central Africa	Usually not considered to be a valid genetic group (Trask, 1996). Recognised by Greenberg (1963). Nichols (1997) considers the following language groups in this phylum to form a quasi-stock or structural pool: Nilotic, Nubian, Central Sudanic, Kunama-Ilit, Koman-Gumaz and Kadugli. She excludes Sonrai, Saharan, Maban, Fur and Berta. Ruhlen (1987) classifies Kadugli as a Niger-Kordfanian language.
Uralic-Yukaghir	Europe, Asia	Uralic accepted. Yukaghir usually accepted to be related to Uralic (Blench and Spriggs, 1997; Trask, 1996)

2.4 Conclusions

The human species is sub-divided into local populations which tend to be largely endogamous. People usually marry locally, especially hunter-gatherers and horticulturalists. Gene flow is much reduced by distance. Long distance gene flow was rare until recently. The history of modern humans has been characterised by population expansion, fission and divergence. The genetic similarity among human populations is a consequence of their recent common origin. To a large degree, genetic trees reflect these demographic events. Language trees also reflect population history.

Chapter 3

Statistical methods for evolutionary inference used in this thesis

3.0 Summary

Genetic and linguistic trees were used as models of the past relationships among populations, to identify independent evolutionary events. Multiple and logistic regression were used to investigate the nature of the transmission of biocultural traits among populations. This was done by comparing the effect, on a trait in the sample, of that trait in each population's nearest neighbours and genetic relatives.

Phylogenetic comparative methods, used to test for correlated evolution among variables, included Felsenstein's (1985) method of comparative analysis using independent contrasts, and Pagel's (1994) maximum likelihood method for testing for correlated evolution among discrete characters.

3.1 Genetic and linguistic trees used as models of population history

All the statistical methods used in this thesis require an explicit tree model of the past relationships among populations (a population phylogeny). Genetic and linguistic trees were used as models of phylogeny. It is not known which tree is the best representation of the past relationships among populations, so each comparative analysis was repeated using more than one tree.

Genetic trees. Genetic trees were taken from *The History and Geography of Human Genes* by Cavalli-Sforza et al. (1994), the most comprehensive source of information about genetic relationships among populations worldwide. Cavalli-Sforza et al.'s methods for constructing their F_{ST} genetic distance trees were described in chapter 2 (section 2.2.3).

On the trees shown in Figures 4.2 and 6.2, the higher nodes (towards the root) follow Cavalli-Sforza et al's worldwide F_{ST} distance tree (Fig. 2.3.2.B, Cavalli-Sforza et al., 1994:78). The lower nodes (towards the tips) follow Cavalli-Sforza et al.'s F_{ST} distance trees for individual continents or sub-continental regions (Figs. 3.5.1, 4.10.1, 4.11.1, 4.13.1, 4.14.1, 4.15.4, 6.9.1, 6.10.1, 6.10.3, 7.8.1, Cavalli-Sforza et al., 1994). Where there were conflicts among the source trees in Cavalli-Sforza et al., the tree in which populations were distinguished at a lower level was used. On the tree shown in

Figure 4.3, the higher nodes follow a tree constructed using a measure of genetic distance developed by Nei (Fig. 2.3.2A, Cavalli-Sforza et al., 1994:78). Lower nodes follow Cavalli-Sforza et al's F_{ST} genetic distance trees for individual continents or sub-continental regions. The African genetic tree shown in Figures 5.8a and 5.8b follows Cavalli-Sforza et al's F_{ST} genetic distance tree for Africa (Fig. 3.5.1, Cavalli-Sforza et al., 1994).

Language trees. Language trees in this thesis follow the language classifications of Ruhlen (1987). A single origin of languages was assumed. Some language synonyms were identified from Voeghlin and Voeghlin (1977).

Ruhlen's (1987) classification of languages is a composite classification derived from many sources. It has the merit of being comprehensive (including most of the world's languages) and well resolved (i.e. tree-like). Voeghlin and Voeghlin's (1977) language classification is even more comprehensive, but the relationships among languages are less well resolved. Because Ruhlen's language classifications are derived from numerous sources, they were constructed using many different methods of linguistic reconstruction (see chapter 2, section 2.3.2). I have not resolved any language trees above the phylum level recognised in Ruhlen (1987). In other words, I have not incorporated any of the hypothesised higher-level language groups, such as Nostratic and Eurasiatic, in linguistic trees in this thesis, because these super-phyla are highly controversial among linguists (Ruhlen, 1991). The language trees used in this thesis are therefore unresolved at the higher nodes. Language trees used in this thesis are shown in Figures 4.5, 5.4-5.7, 5.14, 5.15, 6.4 and 6.7.

Composite trees. Pagel's (1994) method of phylogenetic comparative analysis requires a fully resolved phylogeny (see section 3.2.2). In order to use this comparative method, fully resolved, composite phylogenies were constructed (Figures 4.7, 4.8, 5.11 and 5.12). These trees were based on Cavalli-Sforza et al.'s (1994) F_{ST} genetic trees. Unresolved nodes were resolved on language where possible. Where a multiple node could not be resolved using language, and there was no variation in the characters being tested, populations in this node were pooled.

Branch lengths. Branch lengths on all trees were assumed to be equal.

3.2 Phylogenetic comparative methods

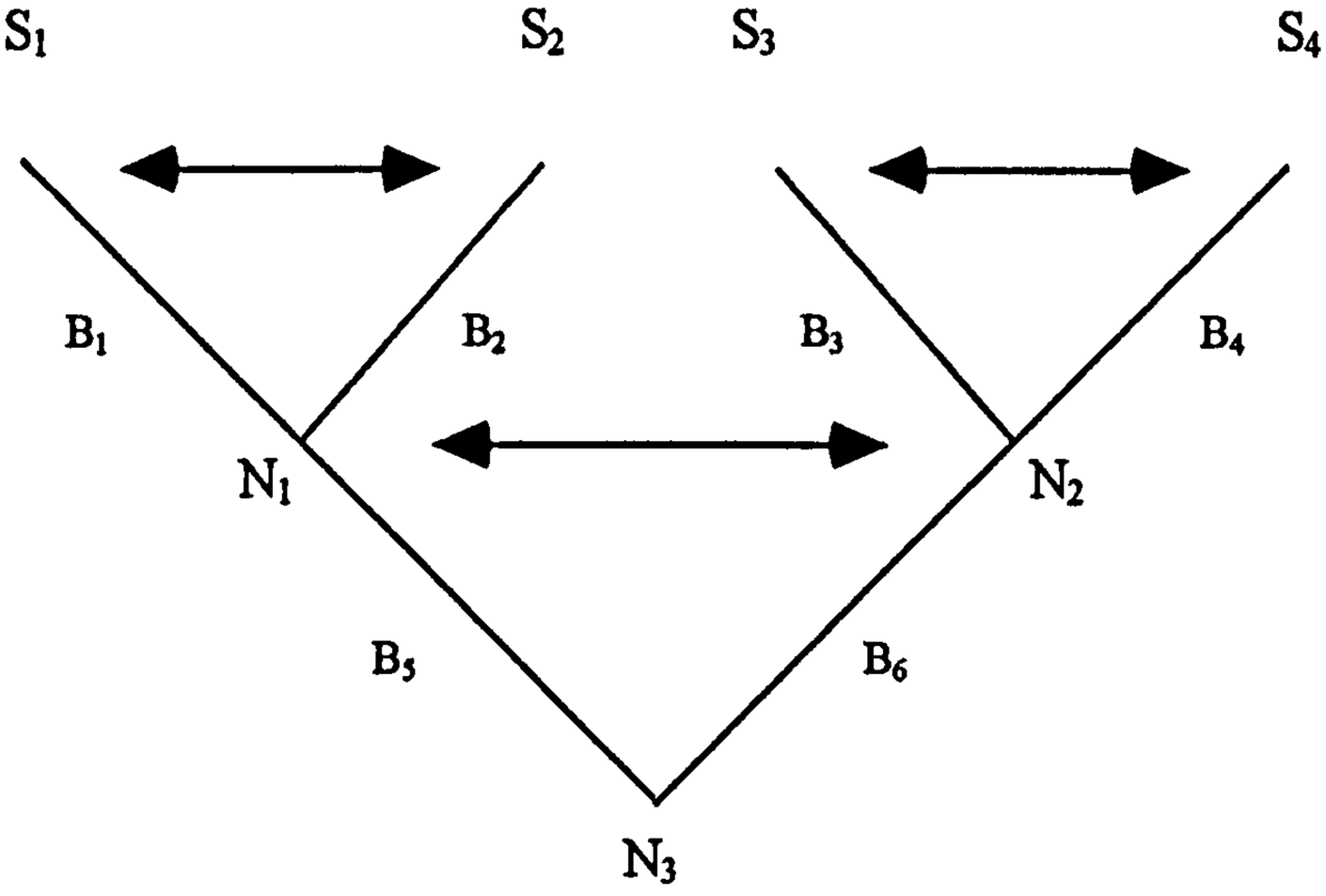
Phylogenetic comparative methods use independent evolutionary events (changes in variables) as data points, to test a hypothesis that two or more variables are related. Two phylogenetic comparative methods were used. The first was phylogenetic comparative analysis using independent contrasts (Felsenstein, 1985; Pagel, 1992), used to test for correlated evolution among continuous variables, or between a categorical dependent variable and continuous independent variables. The second was Pagel's (1994) method of testing for correlated evolution among discrete traits.

3.2.1 Comparative analysis using independent contrasts

The method of comparative analysis using independent contrasts was first developed by Felsenstein (1985). In this method, species or populations are placed on a phylogeny, which is a tree representing the past relationships among populations. Internal nodes on the tree represent ancestral populations. One tests for correlated evolution among variables along the branches of a phylogeny (Felsenstein, 1985; Harvey and Pagel, 1991; Pagel, 1992). This method was used in chapters 4, 5 and 6.

Evolutionary change within populations descending from a single node is independent. This is illustrated in Figure 3.1, which shows four species (S_1, S_2, S_3 and S_4) placed on a phylogenetic tree. The three internal nodes on the tree are called N_1, N_2 and N_3. The six branches (representing divergent populations) are called B_1 to B_6. Evolutionary change along branches descending from a single node is independent. For example, evolutionary change in B_1 is independent of evolutionary change in B_2 (both descending from N_1) (Felsenstein, 1985).

Figure 3.1 Independent contrasts on a phylogenetic tree



Independent contrasts are differences in character states between taxa which descend from a single node, for example S_1 and S_2 (descending from N_1) or N_1 and N_2 (descending from N_3). Independent contrasts on the tree in Figure 3.1 are indicated by arrows. Independent contrasts in the dependent variable are calculated by subtracting the smaller variable from the larger variable, so that contrasts in the dependent variable are always positive. Contrasts in independent variables are calculated by subtracting in the same direction as for the dependent variable. To calculate contrasts across internal nodes on the tree, ancestral character states (at internal nodes of the tree) are estimated from character states in extant populations (at the tips of the tree). A model of evolution by Brownian or random motion was used, in which the net change in a character along a branch is expected to be zero, with variance

proportional to the branch length (Felsenstein, 1985; Pagel, 1992; Purvis and Rambaut, 1995). If the branches are of equal length, then the character state at the higher node is equivalent to the mean of the character states at the immediately lower nodes. If branch lengths are not equal, the longer branch is given less weight in estimating the ancestral character state, because the probability of change in the character state between the 'mother' populations and the 'daughter' population is higher (Felsenstein, 1985; Pagel, 1992; Purvis and Rambaut, 1995). For a bifurcating tree, the number of contrasts is equal to the number of populations in the sample minus one. Each independent contrast contributes one degree of freedom when calculating the significance of relationships between variables. Independent contrasts were generated using the computer program CAIC (Purvis and Rambaut, 1995).

Testing for correlated evolution among variables. The relationship between contrasts in different variables can be investigated using standard statistical tests. If evolutionary change in two characters is correlated, then contrasts in those variables will be positively correlated. If evolutionary change in two characters is negatively correlated, then contrasts in those variables will be negatively correlated. For continuous variables, regression through the origin can be used to estimate the 'evolutionary regression coefficient' – the amount of change in the dependent variable predicted from a given amount of change in an independent variable (Pagel, 1993). The regression is through the origin because the independent contrasts are differences in character states, not actual character values (Felsenstein, 1985; Pagel, 1992).

It is also possible to use independent contrasts to test for correlated evolutionary change if the dependent variable is categorical (see chapter 5). In this case, independent contrasts are only generated at nodes on the tree where changes in the discrete variable occur. Again, positive contrasts in the dependent variable are calculated. Under the null hypothesis of no relationship between the variables, contrasts in the independent variable at these nodes are expected to have a mean of zero. A single sample t-test (alternatively a sign test) can be used to test whether the mean of the independent contrasts in the continuous variable differs from zero (Purvis and Rambaut, 1995). Comparative analysis using independent contrasts cannot be used to test the relationship between two or more categorical variables.

Multiple nodes. Felsenstein's (1985) method of comparative analysis using independent contrasts was designed for a bifurcating phylogeny. But multiple nodes, or polytomies, are often present on genetic or linguistic trees. Most multiple nodes are 'soft' polytomies, meaning that the true phylogeny is bifurcating, but the data from which the tree was constructed were too incomplete to allow the true, dichotomous branching relationship among populations to be distinguished. This can be contrasted with 'hard' polytomies, which show a true branching pattern among species, and occur when three or more species split from an ancestral species simultaneously. In nature, this is probably rare.

Multiple nodes were resolved using the method of Pagel (1992). In this method, it is assumed that variation within a multiple node evolved since the taxa in that node split from their common ancestor (the node from which they descend). Taxa within multiple nodes are divided into two groups (called 'expanding the node' by Pagel,

1992), and a contrast is calculated between the weighted average of the variables in each group. Multiple nodes were split into two groups so as to maximise the variation between the two groups in a chosen variable, called the 'special variable' by Purvis and Rambaut (1995). If the dependent variable was categorical, it was used as the special variable (Purvis and Rambaut, 1995). If all variables were continuous, one continuous variable was chosen to be the special variable, either the variable thought to best represent population history (in chapter 4) or the variable hypothesised to be causal in the hypothesis being tested (in chapter 6). In such cases, it may be questionable which criterion is best for resolving unresolved nodes (Pagel, 1992). In chapters 4 and 6, the analysis was repeated using alternative special variables, and it made no difference to the results.

Pagel's (1992) method for resolving unresolved nodes enables one to use variance within multiple nodes in the comparative analysis. Where was there is variation in the special variable within a multiple node, one independent contrast (one degree of freedom) is generated from each multiple node.

Computer simulations of the method of comparative analysis using independent contrasts. Martins and Garland (1991, reported in Pagel, 1992) tested Felsenstein's (1985) method of comparative analysis using independent contrasts on a bifurcating phylogeny. In a simulation in which branch lengths on the tree were proportional to time, there was a Type 1 error rate (meaning that a positive relationship was found where there was no relationship in the data) of 0.05, compared to an expected rate of 0.05. In a simulation in which real branch lengths varied, but a simplified model of equal branch lengths was used (as in this thesis), the Type 1 error rate was 0.08,

compared to an expected rate of 0.05. Gittleman and Luh (1992) tested Pagel's (1992) method for resolving multiple nodes, using computer simulations, and found a Type I error rate of 0.05, compared to an expected rate of 0.05.

3.2.2 A maximum likelihood method for testing for correlated evolution among discrete characters

Pagel (1994) described a method for testing for correlated evolution in two discrete characters on a phylogeny using maximum likelihood. This method was used in chapters 4 and 5. Unlike comparative analysis using independent contrasts, this method does not rely of a single set of reconstructed character states. Instead, it represents all character states at internal nodes on the tree as probability distributions. Therefore, all possible transitions in character states on the phylogeny can be taken into account when calculating the likelihood of different models of evolution.

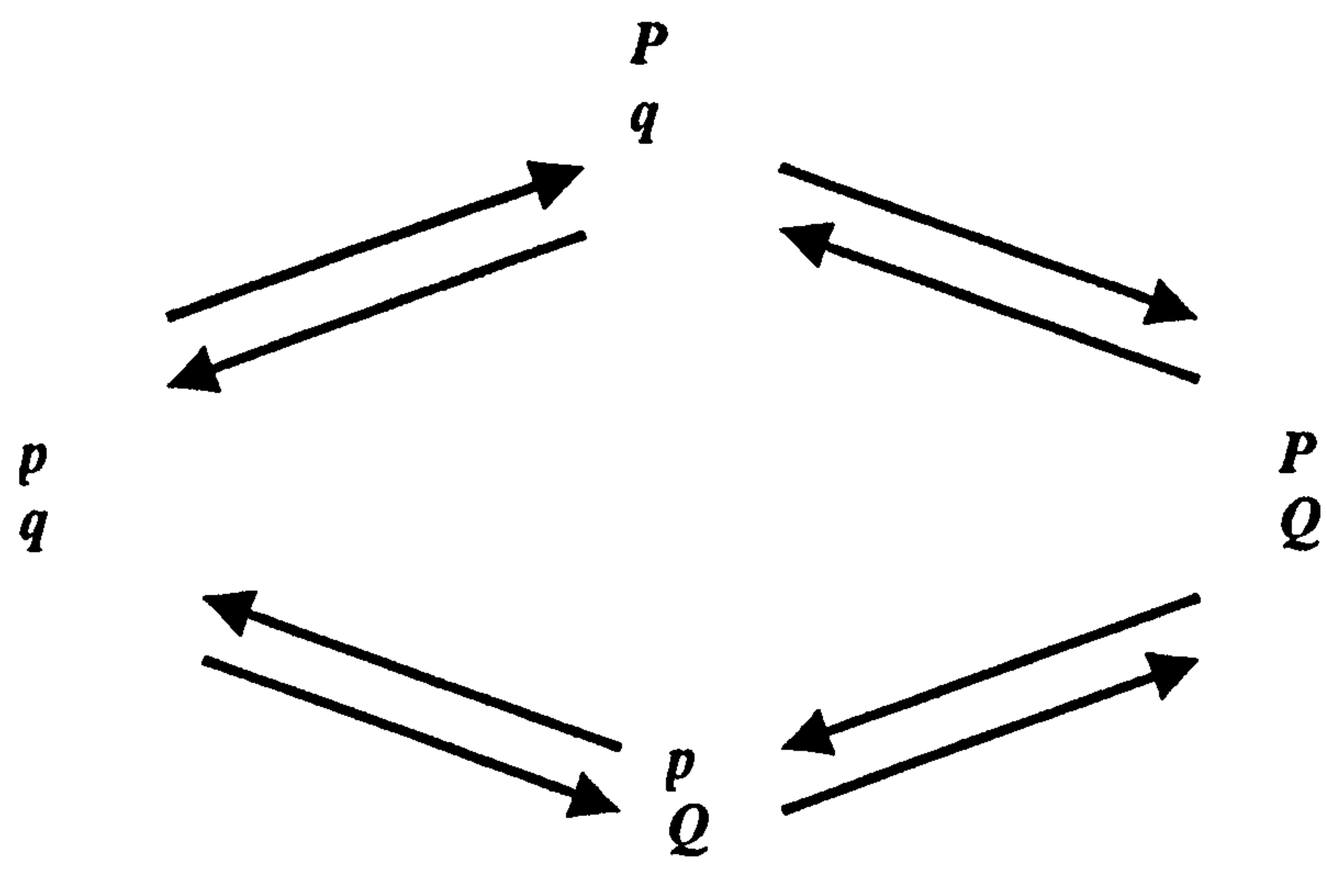
This method tests the hypothesis that evolutionary change in two variables is correlated, by comparing the fit of two models to the data. The first model is an independent model, in which the two characters evolve independently along the branches of a phylogeny. The second model is a dependent model, in which change in the two characters is correlated. The goodness of fit of the two models is compared, using a likelihood ratio (LR) statistic, defined as:

$$LR = -2\log_e[L(I)/L(D)]$$

where L(I) is the likelihood of the model of independent evolution and L(D) is the likelihood of the model of dependent evolution (Pagel, 1994; 1998). The LR statistic has a chi-square distribution with the number of degrees of freedom equal to the difference in the number of parameters between the two models. The number of parameters in an independent model with two binary characters (P and Q) is four, because there are four possible transitions, P to p, p to P, Q to q and q to Q. The number of parameters in the dependent model is eight, shown in Figure 3.2. If there is a significant difference between goodness of fit of the independent and dependent models to the data (i.e. if the model of correlated evolution fits the data significantly better), this is evidence that evolution in the two characters is correlated (Pagel, 1994;1998).

Figure 3.2 Eight possible transitions in two correlated binary characters

Arrows represent possible transitions. Each of the two characters (*P* and *Q*) exists in two states, *P* and *p*, and *Q* and *q*. In the model only one character state can change at a time. For example, to go from *pq* to *PQ*, either *p* could change first (*pq* changes to *Pq*, then *Pq* changes to *PQ*) or *Q* could change first (*pq* changes to *pQ*, then *pQ* changes to *PQ*).



Causality in correlated evolutionary change. Pagel's (1994) maximum likelihood model can also be used to estimate the probable direction of evolutionary change in two characters. This provides an insight into causality among characters, because if one character, *A*, consistently evolves before another character, *B*, then it is unlikely

that change in *A* is caused by change in *B*. In Pagel's (1994) method, it is possible to fix the rate of one of these transitions to zero. The importance of each transition in the model of correlated evolution (Figure 3.2) is assessed by comparing the goodness of fit of the unrestricted model of correlated evolution (the full dependent model), with a restricted model, in which the rate of one of the eight possible transitions has been set to zero. The restricted and unrestricted models are compared using a likelihood ratio statistic. If the goodness of fit of the model of restricted evolution is significantly less good than the full model, this is evidence that this transition is significant.

Pagel's (1994) maximum likelihood method was implemented using the computer program DISCRETE (available from Mark Pagel, University of Reading). At present, this program requires a bifurcating phylogeny (see section 3.1 for the trees used for this method).

3.3 A method for investigating the transmission of traits among populations

Genetic and cultural traits can be transmitted between neighbouring populations (horizontal transmission) as well as from mother to daughter populations (vertical transmission). Here I describe a method which was intended to test whether traits are transmitted vertically or horizontally, or both.

It was tested whether each trait was associated with a population's closest phylogenetic relatives and/or its nearest geographical neighbours. If a trait is associated with phylogenetic relatives this indicates that it is transmitted vertically, from mother to daughter populations. If a trait is associated with nearest geographical neighbours this indicates that it is transmitted horizontally, between neighbouring populations.

Defining phylogenetic relatives. Phylogenetic relatives were defined as the genetic sister-group of each population on a genetic or a linguistic tree. In many cases a population could be compared to a single other population, with which they formed a paired clade at the tips of the tree. In cases where three or more daughter populations descended from a single node, each population was compared to all the other populations in the clade. In some cases a population was co-ordinate with a larger clade. In these cases the population was compared to all populations in the co-

ordinate clade. For discrete variables, the multiple node was counted as having a given character state if 50% or more of the populations in the node had that character state. For continuous variables, the mean value of each trait for all the other populations in the co-ordinate clade was used.

Defining nearest neighbours. Nearest geographical neighbours were found using great-circle distances. Great-circle distances were calculated using a method and computer program written by Rob Baulk (Appendix 1). Each population was compared to the same number of phylogenetic relatives and geographical neighbours. Thus, populations which were compared to a single phylogenetic relative were also compared to a single geographical neighbour (the nearest population). Populations compared to two or more phylogenetic relatives were compared to an equal number of their nearest geographical neighbours. For continuous variables, where populations were compared to more than one geographical neighbour, the mean of value of each trait in the geographical neighbours was used. For discrete variables, the neighbouring group was counted as having a given character state if 50% or more of the populations in the neighbouring group had that character state.

Defining phylogenetic relatives and nearest neighbours in chapter 4. The method used to define nearest neighbours and phylogenetic relatives in chapter 4 differed in three respects from the method used in chapters 5 and 6, as the method was revised with each analysis. The differences are not substantial, and they are not thought to have made any difference to the results. The first difference was that, in chapter 4, to define the closest phylogenetic relatives where a population was co-ordinate with a multiple node, the mean value of the character in the multiple node was weighted

using branch lengths. In chapters 5 and 6, branch lengths were not used to weight mean values in this way, because geographical neighbours were not weighted by relative distance. Second, straight line distances using an atlas, rather than great circle distances, were used to identify nearest geographical neighbours. Third, populations were compared to the same *average* number of phylogenetic and geographical neighbours, but each individual population was not compared to the same number of each. The mean number of phylogenetic relatives to which each population was compared was 2.8. Each analysis was repeated three times, using 1, 2 and 3 nearest geographical neighbours. In chapters 5 and 6, each individual population was compared to the same number of phylogenetic and geographical neighbours in order to make the comparison more exact.

Comparing the effects of phylogeny and geography on character states. Regression was used to test the predictive effect of character states in phylogenetic relatives and geographical neighbours (the independent variables) on character states in populations in the sample (the dependent variable). All regressions were done using SPSS (Norušis, 1994).

Continuous variables. Multiple regression was used to test whether continuous variables were associated with phylogeny and/or geography. Each character was tested separately. The dependent variable was the character state being tested for each population in the sample. The independent variables were a) the character state in each population's phylogenetic sister-group, and b) the character state in each population's nearest geographical neighbours.

Categorical variables. For categorical variables, logistic regression was used to test whether the trait was associated with phylogeny and/or geography. Discrete variables with more than two character states were recoded as binary variables (present/absent) (Norušis, 1994). One new variable was created for each character state tested, a binary variable showing presence or absence of that character state. If 50% of cultures each had one character state then both character states were counted as present. In the logistic regression, the dependent variable was the character state (present or absent) of the character being tested in each population in the sample. The independent variables were a) the character state (present or absent) in each population's phylogenetic sister-group, and b) the character state (present or absent) in each population's nearest geographical neighbours.

Chapter 4

Pastoralism and the evolution of lactase persistence[2]

4.0 Summary

In most of the world's population the ability to digest lactose declines sharply after infancy. High lactose digestion capacity in adults, prevalent in northern Europe and among pastoralists of the Circum-Mediterranean, is thought to be an evolutionary adaptation to millennia of drinking milk from domestic livestock. Milk can also be consumed in a processed form, such as cheese or soured milk, which has a reduced lactose content. Two other selective pressures for drinking fresh milk, with a high lactose content, have been proposed: promotion of calcium uptake in high-latitude populations prone to vitamin-D deficiency, and maintenance of water and electrolytes

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[2] An earlier version of this chapter was published as Holden C, Mace R. 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology* 69:605-628, which was awarded the Gabriel G. Lasker prize for the most significant paper published in the journal *Human Biology* in 1997.

in the body in highly arid environments. All three hypotheses are supported by the geographical distribution of high lactose digestion capacity in adults. But lactose digestion capacity and the variables hypothesised to be associated with it (pastoralism, aridity and solar intensity) have a strong association with phylogeny, so populations cannot be treated as independent data points when testing the hypotheses comparatively. The hypotheses were tested here using phylogenetic comparative methods. The results support the hypothesis that high adult lactose digestion capacity is an adaptation to dairying, but do not support the hypotheses that lactose digestion capacity is additionally selected for either at high latitudes or in highly arid environments. Pagel's (1994) maximum likelihood method was used to show that the evolution of milking preceded the evolution of high lactose digestion in adults.

4.1 Lactose digestion capacity in adults

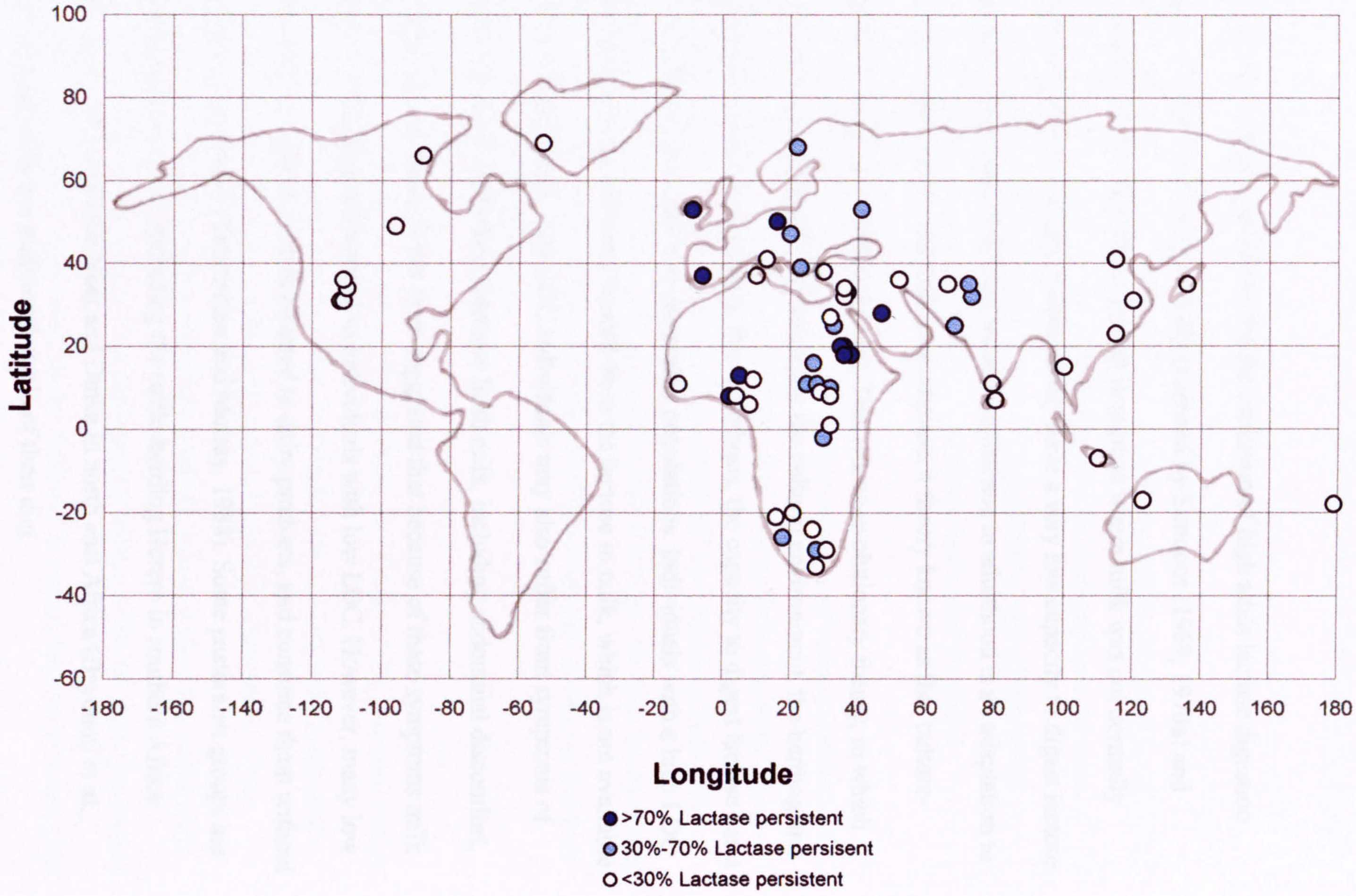
The ability to digest lactose in adults is a genetic polymorphism, inherited as a dominant genetic trait (Sahi et al., 1973; Johnson et al., 1977; Ransome-Kuti et al., 1975; Metneki., et al 1984). The physiological cause of high lactose digestion capacity in adulthood (HLDC) is the retention of high levels of lactase in the small intestine beyond infancy (lactase persistence), which contrasts with the standard mammalian developmental pattern of a steep decline in small intestine lactose levels after infancy (Flatz, 1987).

The prevalence of HLDC varies widely between different ethnic groups. The lactose digestion capacity of over 20,000 individuals worldwide has been tested. HLDC is found at high frequencies (>70%) across north and west Europe, from Ireland to Scandinavia (not including the Lapps). HLDC is also found at high frequencies (>70%) in some pastoralist populations in Africa and the Middle East, including Bedouin camel herders in the Middle East and the Sahara, Tuareg pastoralists in the Sahara-Sahel, Beja pastoralists in north-east Africa, and the cattle-herding Tutsi in east Africa.

Intermediate frequencies of HLDC (30%>70%) are found in populations around the Mediterranean, and in parts of south Asia in Afghanistan, Pakistan and north India. Intermediate HLDC frequencies are also found in some African pastoralist or agro-pastoralist groups, such as the Baggara nomads and Nubian pastoralists in north-east Africa, and the Sotho and the Nama in southern Africa. Patchy sampling in much of sub-Saharan Africa, and south- and central Asia necessitate caution in our overview of these areas, particularly since the distribution of the adult lactose digestive capacity in these regions appears to be locally variable and complex.

Low frequencies of HLDC are found throughout the rest of the world, including many parts of Africa, east and south-east Asia, and in the native populations of America, Australia and the Pacific. The geographical distribution of HLDC in 64 populations included in the present analysis is shown in Figure 4.1 (see also Table 4.1). In Figure 4.1 the frequency of HLDC has been grouped into three levels (>70%, 30-70% and <30% HLDC) for illustrative purposes.

Figure 4.1 Lactase persistence in 64 populations worldwide



4.1.1 Selective pressures for drinking milk

There are three major hypotheses for the evolution of high adult lactose digestion capacity. The first was independently proposed by Simoons (1969; 1970a) and McCracken (1971). They observed that in regions where milk was not normally consumed until very recently, adults mostly have a very low capacity to digest lactose. It was therefore hypothesised that lactase persistence in adulthood is an adaptation to millennia of pastoralism and milk consumption, a theory known as the 'culture-historical' hypothesis (Simoons 1970a). This is a co-evolutionary theory, in which selection of a genetic trait is influenced by the cultural environment, the herding and milking of livestock. According to this hypothesis, the capacity to digest lactose has a selective advantage to adults in pastoralist populations. Individuals with a high LDC are able to derive a nutritional benefit from the lactose in milk, which is not available to low LDC individuals. Low LDC individuals may also suffer from symptoms of lactose intolerance when they consume fresh milk, including abdominal discomfort, flatulence and diarrhoea. It has been suggested that because of these symptoms milk could be nutritionally detrimental to individuals with low LDC. However, many low LDC individuals can become habituated to dairy products, and consume them without experiencing symptoms (Scrimshaw and Murray, 1988). Some pastoralist groups are predominantly low LDC, including the cattle-herding Herero in southern Africa (Currie et al., 1978) and the Nuer and Dinka in north east Africa (Bayoumi et al., 1982), although milk is a traditional staple of their diet.

Populations which keep livestock but do not milk them are found in China and SE Asia and parts of sub-Saharan Africa (Murdock, 1967; Simoons, 1970b). In later modifications of his hypothesis, Simoons (1979) argued that high LDC would not be selected for in these populations.

Milk can be processed into a variety of dairy products, such as cheese and yoghurt. These dairy products have a lower lactose content than fresh milk, so are more digestible for low LDC individuals. Two further hypotheses regarding specific advantages of fresh milk, with a high lactose content, have been proposed.

Flatz and Rotthauwe (1973) suggest that there is a selective advantage to drinking fresh milk at high latitudes, where sunshine is limited, especially in winter, and humans are at risk of vitamin D deficiency and rickets. The lactose in fresh milk promotes the uptake of calcium, also present in milk (Durham, 1991; Scrimshaw and Murray, 1988). This hypothesis could explain the high frequency of lactose digesters in northern European populations.

The third hypothesis, by Cook and Al-Torki (1975; also Cook 1978), proposes that in highly arid environments the water content of fresh milk, as well as the nutritional value of lactose, would have increased the survival high LDC individuals. They hypothesised that diarrhoea and consequent water depletion in low LDC individuals would have reduced their fitness. This hypothesis is supported by the high frequencies of adults with the lactose digestion capacity observed in pastoralist groups in hot, arid regions in the Middle East and Africa, such as Bedouin, Tuareg, and pastoral Fulani (see Table 4.1).

The evolution of adult lactase persistence has been modelled several times. Bodmer and Cavalli-Sforza (1976) estimated that a selection coefficient of 0.04 would be necessary for high LDC to increase from an initial prevalence of 0.001% to the levels observed today in northern European populations (estimated frequency 0.5) within 290 generations (9,000 years). If the initial frequency of the lactase persistence gene were 1.0%, a selection coefficient of only 0.015 would be required. This time scale is realistic for the Middle East where livestock were first domesticated at around 8-7,000 BC (Clutton-Brock, 1987). Flatz (1987) estimated that for the gene to reach contemporary European levels in the 5,000 years or less since the first known domestic livestock in northern Europe, starting from an initial frequency of 0.005%, a higher selection coefficient of between 3-7% would be required. This calculation was based on the assumption that pastoralism spread by diffusion to indigenous hunter-gatherers in Europe, rather than being introduced by colonisation from Middle Eastern pastoralists (c.f. Ammerman and Cavalli-Sforza, 1984).

More recently, attempts have been made to model the co-evolution of a gene for lactase persistence and the cultural trait of milk drinking. Aoki (1986) estimated that for the selection of the gene for lactase persistence from an initial prevalence of 0.05% to the prevalence observed in northern Europe today (estimated gene frequency 0.7), within the time available since the advent of dairying (6,000 years), and with an effective population size of 500, the selection coefficient must have been greater than 5%. Feldman and Cavalli-Sforza (1989) also found that a selection coefficient of greater than 5% was necessary for a gene frequency of 0.70 to be reached in 6,000 years.

However, in these dual inheritance, co-evolutionary models, milk drinking is a cultural trait with a low initial frequency, whose selection coefficient is dependent on the prevalence of the lactase persistence gene. The ethnographic evidence does not support this assumption, insofar as milk consumption apparently has been universally adopted within some populations with predominantly low lactose digestion capacity, for example the Mongols, the Herero, the Nuer and the Dinka (Table 4.1). Milk-based pastoralism may be the best means of subsistence, particularly in dry, marginal environments, even for lactose non-digesters. Milk processing, and the consumption of fresh milk only in small quantities, are cultural and behavioural means by which many low LDC individuals manage to consume milk products without suffering the symptoms of lactose intolerance. After milk-based pastoralism has been adopted as a means of subsistence, high lactose digestion capacity would be selected for, because it would enable adults to consume more fresh milk and to derive a nutritional benefit from the lactose component of fresh milk. The 'initial' frequency of the cultural trait of milk consumption may therefore be virtually 100%, which could reduce the selection coefficient required for the lactase persistence gene to reach observed frequencies in the time available. In this case these traits would not be truly co-evolutionary, because selection for milk consumption would not be dependent on the gene for lactase persistence.

4.2 Methods and results

There were three parts to the statistical analysis, a study of the transmission of bio-cultural traits in the analysis among populations (section 4.2.2), a test of the hypotheses using independent contrasts (section 4.2.3) and a test of the direction of evolutionary change in the co-evolution of pastoralism and lactose digestion capacity (section 4.2.4).

4.2.1 Data

The population samples used in this analysis were taken from comprehensive reviews by Simoons (1978), Flatz (1987), and Sahi (1994) and from a literature search of the science citation index (Bath Information and Data Services) from 1981-1996 using the terms 'lactose absorption' and 'lactose malabsorption'. Sixty-four populations were included in the analysis, using inclusion criteria described below. The populations included in the sample are shown in Table 4.1. Except where stated in Table 4.1, only samples from adults were included.

All populations included in the analysis were found in Cavalli-Sforza et al.'s (1994) *History and Geography of Human Genes*, and therefore can be placed on a world

genetic tree. Cavalli-Sforza et al (1994) only includes 'aboriginal' populations, defined as populations present in their current locations before 1492. Recent migrant populations are excluded, including all non-native Americans and non-aboriginal Australians. All samples of emigrant populations were excluded, to decrease the probability of recent genetic admixture in the dataset. Samples from populations recognised to have mixed ancestry in the original studies were excluded. Since a linguistic tree was also used in this analysis, all samples are also from populations whose language or language group is listed in Ruhlen's *Guide to the World's Languages* (1991). A number of language synonyms were found in Voeghlin and Voeghlin (1977).

All the samples used here come from populations represented in Murdock's (1967) *Ethnographic Atlas*. Data on pastoralism and geographical location were taken from this source. The *Ethnographic Atlas* code for each population is shown in Table 4.1. The Australian Aborigines and Canadian Eskimos are an exception. They are not single *Ethnographic Atlas* cultures, but they are classified as monophyletic genetic groups by Cavalli-Sforza et al. (1994:78, 323). They were traditionally hunter-gatherers without domesticated livestock.

In total, 8, 026 individuals from 64 cultures were included in the data set. The greatest loss of individuals tested for lactase persistence, resulting from the selection criteria outlined above, was from non-aboriginal populations in America and Australia. More importantly for the aims of this study, a number of samples from 'anthropological' populations were unable to be used because these populations are not known genetically, or are not included in the *Ethnographic Atlas.* Anthropologically

interesting populations lost included, among others, the hunter-gatherer Khants from Western Siberia (94% lactose maldigesters, Lember et al., 1995) and several other groups from the former Soviet Union (Sahi, 1994); the pastoralist Kasakhs (Wang et al., 1984); the Roma (Gypsies), (56% lactose maldigesters, Czeizel et al., 1983); and various Indian groups (45% lactose maldigesters in north India, 67% in south India, Tandon et al 1981). The inclusion criteria applied here, however, had the advantage of allowing all populations to be compared using the same source for variables like pastoralism, which had been previously quantified by an independent researcher. It also allowed the use of different trees as models of human evolution, with the same data set of populations in each tree.

An estimate of reliance on domestic livestock, or pastoralism, was taken from Murdock's (1967) *Ethnographic Atlas*. Murdock (1967) estimated of the percentage of dependence on livestock in each population's total subsistence activities. 'Pastoralism' in this analysis is a quantitative cultural trait, not a qualitative category. The mid-point of the *Ethnographic Atlas* estimate was used as a measure of pastoralism here. For example, where Murdock coded a culture's reliance on livestock as 3, i.e. 26-35% of total subsistence activities, this was counted as 30.5% dependence here. The geographical distribution of dependence on pastoralism is shown in Figure 4.2. In Figure 4.2, dependence on pastoralism has been divided into three groups (<30%, 30-50% and >50% dependence) for illustrative purposes. It can be seen that highly pastoralist populations are mostly found in north Africa and the Middle East (for example, Bedouin, Beja and Tuareg). There was little reliance on domestic animals in most of east and south-east Asia, and among Native Americans.

The *Ethnographic Atlas* also states the main type of livestock kept, and whether or not milking was traditionally practised. For this study, domestic animals which cannot be milked, such as pigs and dogs, were not counted. If the main type of animals kept was recorded as pigs or small domestic animals (e.g. dogs), the society is recorded as non-pastoralist (0% dependence). The analysis was repeated twice, firstly including, then excluding, 'pastoralists' who traditionally did not milk their animals. Populations which keep livestock but do not milk them are found in China, south east Asia and parts of sub-Saharan Africa (Murdock, 1967; Simoons, 1970b).

No distinction was made in this analysis between populations which consume predominantly processed, low-lactase forms of milk and populations which consume significant amounts of fresh milk, with a high lactose content. Ethnographic evidence suggests that milk-processing technologies are present in all dairying or pastoralist groups today. In hot climates such as Africa and the Middle East milk is soured naturally if it is left to stand. It seems probable that milk-processing technologies were present very early in the history of milking domestic animals. It is therefore assumed here that all pastoralists have had equally effective milk-processing technology, whether they lived six thousand years ago or more recently. This assumption contrasts with Durham (1991), who argued that the high frequency of HLDC in north African pastoralists is a consequence of their adopting a pastoralist mode of subsistence very early, before the full development of milk-processing technologies.

It was also assumed that all populations with domestic livestock are under selective pressure to digest fresh milk, because of the nutritional benefits of lactose. This

assumption contrasts with Simoons (1978), who argued that some populations (for example, in southern Greece) that have practised dairying for millennia remain predominantly low LDC because they process all their milk into low lactose dairy products like mature cheese.

Aridity was estimated from the number of months per year with less than 50ml rainfall in the area inhabited by each population (using data on rainfall from Pearce and Smith, 1993). Other measures of aridity were tried, including average annual rainfall, and average rainfall in environments above 30 degrees C, but this made no difference to the outcome of the analysis. The sunshine experienced by each population was estimated from the global solar radiation for land at that longitude and latitude (Essenwanger, 1985). Except where stated in Table 4.1, the longitude and latitude of each population was taken from the *Ethnographic Atlas*.

Figure 4.2 Dependence on pastoralism in 64 populations worldwide

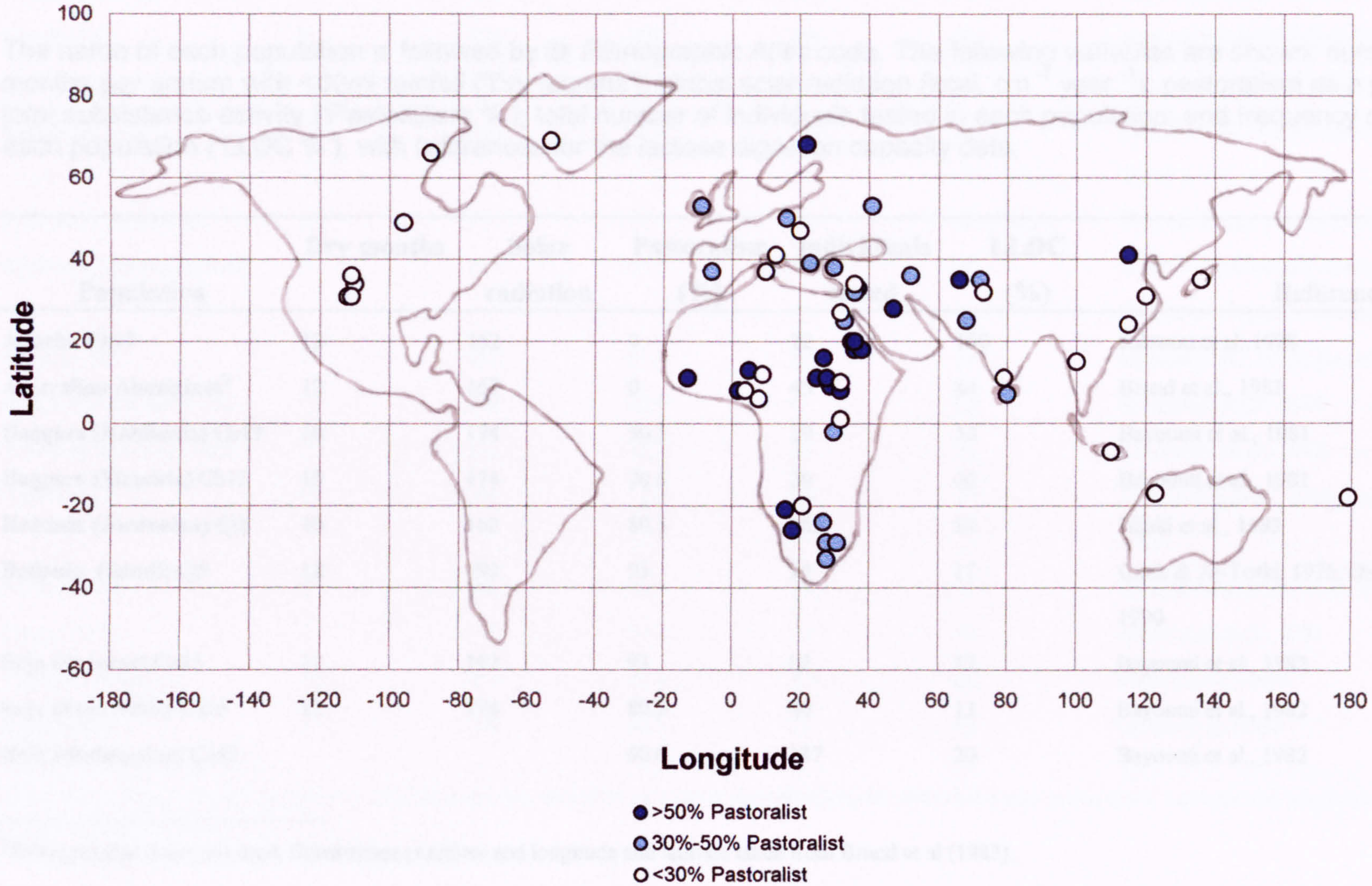


Table 4.1 Lactase persistence in 64 populations worldwide

The name of each population is followed by its *Ethnographic Atlas* code. The following variables are shown: number of months per annum with <50ml rainfall ('Dry months'); global solar radiation (kcal. cm^{-1} $year^{-1}$); pastoralism as a proportion of total subsistence activity ('Pastoralism %'); total number of individuals tested in each population; and frequency of low LDC in each population ('LLDC %'), with references for the lactose digestion capacity data.

Population	Dry months	Solar radiation	Pastoralism (%)	Individuals tested	LLDC (%)	Reference
Apache Nh17	12	162	0	22	100	Johnson et al.,1978
Australian Aborigines[3]	12	167	0	45	84	Brand et al., 1983
Baggara (Habbania) Cb13	10	174	50.5	19	53	Bayoumi et al., 1981
Baggara (Messiria) Cb15	10	174	70.5	20	60	Bayoumi et al., 1981
Bedouin (Jordanian) Cj2	10	162	80.5	162	24	Hijaki et al., 1983
Bedouin (Saudi) Cj5	12	192	93	35	17	Cook & Al-Torki, 1975; Dissanyake et al., 1990
Beja (Amarar) Ca35	12	192	93	82	13	Bayoumi et al., 1982
Beja (Beni Amir) Ca36	12	174	80.5	40	13	Bayoumi et al., 1982
Beja (Haddendoa) Ca43			60.6	137	20	Bayoumi et al., 1982

[3] *Ethnographic Atlas* not used. Subsistence practices and longitude and latitude taken from Brand et al (1983).

Beja (Bisharin) Ca5	12	192	80.5	22	14	Bayoumi et al., 1982
Chippewa Na36	7	124	0	33	97	Newcomer et al., 1977
Czechs Ch3	9	124	30.5	200	13	Madzarovova-Nohejlova, 1974
Dinka Aj11	5	144	50.5	213	76	Bayoumi et al., 1982; Elliott et al., 1973
Egyptians Cd2	12	192	30.5	742	64	Hussein et al., 1982; Hussein and Ezzilarab, 1994
Eskimo (Canadian)[4]	12	79	0	50	82 (>4yrs)	Ellestad-Sayed et al., 1978
Eskimo (Greenland) Na25	8	79	0	119	85	Gudmand-Hoyer and Jarnum,1969; Gudmand-Hoyer et al., 1973; Asp et al., 1975
Fijians[5] Ih4	0	167	0	12	100	Masarei et al., 1972, quoted in Simoons, 1978
Fulani (pastoralist) Cb8	7	174	80.5	9	22	Kretchmer et al., 1971
Fulani (sedentary) Cb22	7	174	40.5	24	71	Kretchmer et al., 1971
Ganda Ad7	0	144	10.5	27	96	Cook and Kajubi, 1966; Cook and Dahlqvist, 1968
Greeks Ce7	8	162	30.5	800	52	Kanaghinis et al.,1974, Ladas et al., 1982
Hausa Cb26	7	174	30.5	17	76	Kretchmer et al., 1971
Hazara Tajiki Ea3	10	162	50.5	79	82	Rahimi et al., 1976
Herero Ab2	9	178	60.5	37	97	Currie et al., 1978

[4]Precise Eskimo group not specified in original study, but all Eskimo groups in the *Ethnographic Atlas* have zero pastoralism. Latitude and longitude taken from Ellestad-Sayed (1978).

[5]6-15% dependence on livestock, but pig-based livestock economy.

Hopi Nh18	10	162	10.5	21	100	Johnson et al., 1978
Hungarian Ch8	7	124	20.5	535	37	Czeizel et al., 1983
Hutu Ae10	2	145	30.5	51	51	Cook and Kajubi, 1966; Cox and Elliott, 1974
Igbo Af10	4	144	10.5	16	81	Elliott et al., 1973; Olatumbosum et al., 1971; Ransome-Kuti et al., 1975
Iranian Ie9	12	162	30.5	40	83 (>12 yrs)	Sadre and Karbasi, 1979
Irish Cg3	0	94	40.5	50	4	Fielding et al., 1981, quoted in Flatz, 1987
Italians (South) Ce5	4	124	10.5	197	67	De Ritis et al., 1970; Burgio et al., 1984; Rinaldi et al., 1984; Cavalli-Sforza et al., 1987
Japanese Ed5	1	162	10.5	66	81	Nose et al., 1979; Shibuya et al., 1970; Yoshida et al., 1975
Javanese (Indonesia) Ib2	1	144	20.5	53	91	Surjono et al., 1973, quoted in Simoons, 1978
Jordanians Cj6	10	162	30.5	204	75	Hijaki et al., 1983; Snook et al., 1976
Lapps Cg4	8	79	60.5	519	41	Isokoski et al., 1981
Lebanese Cj7	5	162	20.5	225	79	Loiselet & Jarjouhi, 1974, quoted in Flatz, 1987; Nasrallah, 1979
Mongols Eb7	10	124	80.5	198	88	Wang et al., 1984
Nama Aa3	9	178	50.5	18	50	Jenkins and Nurse, 1976
Northern Chinese (Han)[6]	8	162	20.5	314	88	Wang et al., 1984; Zheng et al., 1988

[6]Shantung Chinese, Murdock ref. Ed10, Cluster 163, used.

Nubians (Midobi) Cb11	12	174	93	21	67	Bayoumi et al.,1981
Nuer Aj3	5	144	50.5	23	78	Bayoumi et al., 1982
Papago Ni2	10	162	0	14	93	Johnson et al., 1978
Pathans/Pushtu Ea2	10	162	30.5	86	65	Rab and Baseer, 1976; Rahimi et al., 1976
Pima Ni6	10	162	0	62	95 (>4yrs)	Johnson et al., 1977; Johnson et al., 1978
Punjabis Ea13	5	162	20.5	384	56	Rab and Baseer, 1976; Ahmad and Flatz, 1984; Abbas and Ahmad, 1983
Russians Ch11	6	94	30.5	103	57	Lember et al., 1991
San (!Kung and #hua)[7]	9	178	0	65	95	Jenkins et al., 1974; Nurse and Jenkins, 1974
Shilluk Ai6	10	144	20.5	8	63	Bayoumi et al., 1982
Sindhi Ea1	11	192	30.5	45	42	Rab and Baseer, 1976, Ahmad and Flatz, 1984
Sinhalese[8]Eh6	0	144	30.5	158	73	Senewiratne et al., 1977
Sotho Ab8	5	178	30.5	23	65	Segal et al., 1983
Southern Chinese (Taiwan)	4	192	20.5	71	0	Sung and Shih, quoted in Flatz, 1987
Spanish Ce6	5	162	30.5	265	15	Pena Yanez et al., 1971; 1972, quoted in Simoons, 1978
Swazi Ab2	4	192	20.5	12	75	Segal et al., 1983

[7]Nyae Nyae Kung, *Ethnographic Atlas* ref. Aa1, used.

[8]Longitude and latitude of Sri Lanka used, instead of *Ethnographic Atlas* co-ordinates.

Tamils Eg2	0	144	20.5	31	71	Senewiratne et al., 1977
Thai Ej9	4	174	10.5	339	98	Flatz and Saengudom, 1969; Flatz et al., 1969; Keusch et al., 1969; Rotthauwe et al., 1971
Tswana Ab13	6	178	40.5	24	83	Segal et al., 1983
Tuareg (Aulliminden) Cc8	8	144	60.5	118	13	Flatz et al., 1986
Tunisians Cd16	8	162	20.5	43	83	Filiali et al., 1987
Turks Ci5	6	162	40.5	470	71	Flatz et al., 1986
Tutsi Ae10	2	145	40.5	59	7	Cook and Dahlqvist, 1968; Cook and Kajubi, 1966; Cox and Elliott, 1974; Elliott et al., 1973
Xhosa Ab11	3	178	30.5	17	82	Segal et al., 1983
Yoruba Af6	4	144	10.5	100	91	Ktretchmer et al., 1971; Olatunbosun et al., 1971, Ransome-Kuti et al., 1975
Zulu Ab12	3	178	40.5	32	81	Segal et al., 1983

4.2.2 The transmission of traits between populations

Statistical analysis. The transmission of traits in the analysis among populations was investigated, using multiple regression to compare the association of each trait in the sample with that trait in the populations' phylogenetic relatives and geographical neighbours. This method was described in chapter 3.

The phylogenetic sister-group of each population was defined from a genetic tree of the populations in the sample. An F_{ST} genetic distance tree was used (see section 4.2.3). In some cases the phylogenetic sister-group was another population or populations at the tips of the tree. In other cases it was an internal node, in which case character states were calculated using the computer program CAIC (Purvis and Rambaut, 1995). On average each population was compared to 2.83 phylogenetic relatives.

Then the three nearest geographical neighbours for each population were found, following the distribution of the populations on a map (Figs. 4.1 and 4.2). For each of the four variables, an average of the values of these three nearest populations was calculated. This created the 'nearest neighbours' value for each variable. The analysis has been repeated with 1, 2 and 3 nearest geographical neighbours. This did not make any difference to the results. Only the results using 3 geographical neighbours are reported here. The average number of phylogenetic relatives and geographical neighbours is thus nearly the same (2.83 and 3 respectively).

Multiple regression was used to test the relationship between character states in the sample (the dependent variable) and in each population's closest phylogenetic relatives and three nearest neighbours (the independent variables).

Results. The results are presented in Table 4.2. Lactose digestion capacity is significantly associated with both the nearest neighbour and the phylogenetic sister group. This suggests that this gene is transmitted both vertically within populations and horizontally between neighbouring populations. Pastoralism is highly significantly associated with phylogenetic sister-groups' pastoralism, but not with nearest-neighbours' pastoralism, suggesting that transmission of this trait is mostly vertical. Aridity is also associated with phylogenetic sister-group but not with nearest neighbours, suggesting that with respect to this environmental variable, daughter populations tend to inhabit similar environments to their ancestors.

Solar intensity is largely a function of latitude, and nearest neighbours are defined using longitude and latitude, so an association between solar intensity and nearest neighbours is probably inevitable. Solar intensity was found to be highly significantly associated with both genetic sister-group's values and with nearest-neighbours' values. Ignoring the association with geography (because the two variables are confounded), the association with phylogeny again suggests that 'daughter' populations tend to remain in a similar geographical location to their ancestors.

It is concluded that all four traits cluster in a non-random way with respect to phylogeny, and therefore that it is necessary to apply phylogenetic comparative

methods to this problem. It is also interesting that pastoralism (a cultural trait) is the trait which appears to be transmitted most strongly from the older to the younger generation within a population group, rather than being passed horizontally between neighbouring populations. It is often assumed that cultural or behavioural traits are more labile, and more likely to be transmitted by horizontal diffusion, than genetic traits, but this does not seem to be the case for pastoralism. The phylogenetically conserved character of pastoralism was also found using a different method by Guglielmino et al. (1995) (see chapter 1).

Table 4.2 The transmission between populations of bio-cultural traits

Multiple regression results, showing the association of each trait with phylogeny (phylogenetic relatives) and geographical proximity to other populations (three nearest neighbours). The significance values shown are of partial regression coefficients. All multiple regressions were highly significant overall (F significant at $p<0.0001$).

	Phylogenetic relative(s)			Geographical neighbour(s)		
Dependent variable	**Slope**	**S.E. of slope**	**Significance of slope**	**Slope**	**S.E. of slope**	**Significance of slope**
Per cent high LDC	.40	.16	0.02	.39	.19	0.05
Pastoralism	.63	.13	<0.0001	.15	.16	n.s.
Aridity	.48	.16	0.004	.30	.20	n.s.
Solar radiation	.34	.12	0.01	.84	.15	<0.0001

4.2.3 Testing the hypotheses using independent contrasts

Statistical analysis. Phylogenetic comparative analysis using independent contrasts was used to test the three hypotheses (Felsenstein, 1985; Pagel, 1992). The relationship between contrasts in lactose digestion capacity and pastoralism, aridity and solar intensity was tested using multiple regression. Independent contrasts (measures of change at each branch of the tree) were generated after the method of Felsenstein (1985) and Pagel (1992), implemented by the computer program CAIC (Purvis and Rambaut 1995). The regression is through the origin (Pagel 1992). The slopes show the predicted amount of evolutionary change in the dependent variable, per unit of change in each independent variable. All the branch lengths on the trees were assumed to be are equal. Lactose digestion capacity was used as the special variable to resolve unresolved nodes because as a genetic trait it was thought to best represent population history.

Two alternative genetic trees were tested, both adapted from Cavalli-Sforza et al (1994). These two trees were constructed using different methods of calculating genetic distance. The first is an F_{ST} genetic distance tree, shown in Figure 4.3. On this tree, higher nodes (towards the root) follow Cavalli-Sforza et al.'s (1994) F_{ST} tree of the world. Lower nodes (at the tips) follow trees of individual continents in Cavalli-Sforza et al. The second tree was based on a modified Nei genetic distance tree,

adapted from Cavalli-Sforza et al. (1994:78). Lower nodes follow (F_{ST}) trees of individual continents in Cavalli-Sforza et al. This tree is shown in Figure 4.4. The cultural descent of populations was modelled using a language tree based on the classifications of Greenberg, taken from Ruhlen (1991), and assuming a monophyletic origin of language (Fig. 4.5). The world language phylogeny used here is less resolved than the genetic trees, because of the lack of resolution above the language phyla level. Because language evolves much more rapidly than genes, similarities resulting from deep historical relationships are generally considered to be completely obscured after about 10,000 years of divergence (although see Cavalli-Sforza et al., 1988; and Ruhlen, 1991 for an opposing argument). Due to the lack of resolution back through time, using the language tree was rather similar to using a test only involving the tips of the genetic trees.

Results. Figures 4.3 and 4.4 show the two alternative genetic trees used in the analysis. Figure 4.3 also shows the variation in lactose digestive capacity in populations throughout the world, divided into high, medium, and low prevalence of high LDC for illustrative purposes, and mapped onto the tree using parsimony (using the computer program MacClade, Maddison and Maddison, 1992). High prevalence of high LDC are mostly clustered within the Indo-European – North African clade. Apparently independent instances of evolution of high lactose digestion capacity occur scattered throughout the sub-Saharan African clade. As expected from the geographical distribution of this trait, high lactose digestion capacity is virtually absent in the SE Asian, east Asian and native American clades.

Dependence on livestock in populations throughout the world is shown mapped onto

a tree in Figure 4.4. The pattern of livestock dependence is broadly similar to the distribution of lactose digestion capacity, but pastoralism is more widespread than high levels of lactase persistence. The root of the Indo European – North African clade shows a moderate to high dependence on livestock (the ambiguity represented by the hatched lines indicates that it is uncertain whether this dependence was high or moderate). This is consistent with archaeological evidence of the antiquity of domestic livestock in the Middle East and north Africa (Clutton-Brock, 1987; Sherratt, 1980). In sub-Saharan Africa the root of the Bantu – Nilotic clade shows a moderate to high dependence on livestock, but pastoralism is absent from deeper nodes within the sub-Saharan part of the tree.

In the comparative analysis using independent contrasts, for all trees, reliance on pastoralism was significantly associated with variance in lactose digestion capacity among populations worldwide (Table 4.3). Neither solar radiation, nor dry months per year, was significantly associated with variation in lactase persistence.

It did not make a significant difference to the results whether the populations which traditionally kept livestock but did not milk their animals were counted as pastoralists or not. Counting these populations as non-pastoralist slightly increased the association between pastoralism and HLDC, as the culture-historical hypothesis predicts (Simoons, 1979) but the significance level of the result was not changed. These populations formed a very small proportion of the populations included here.

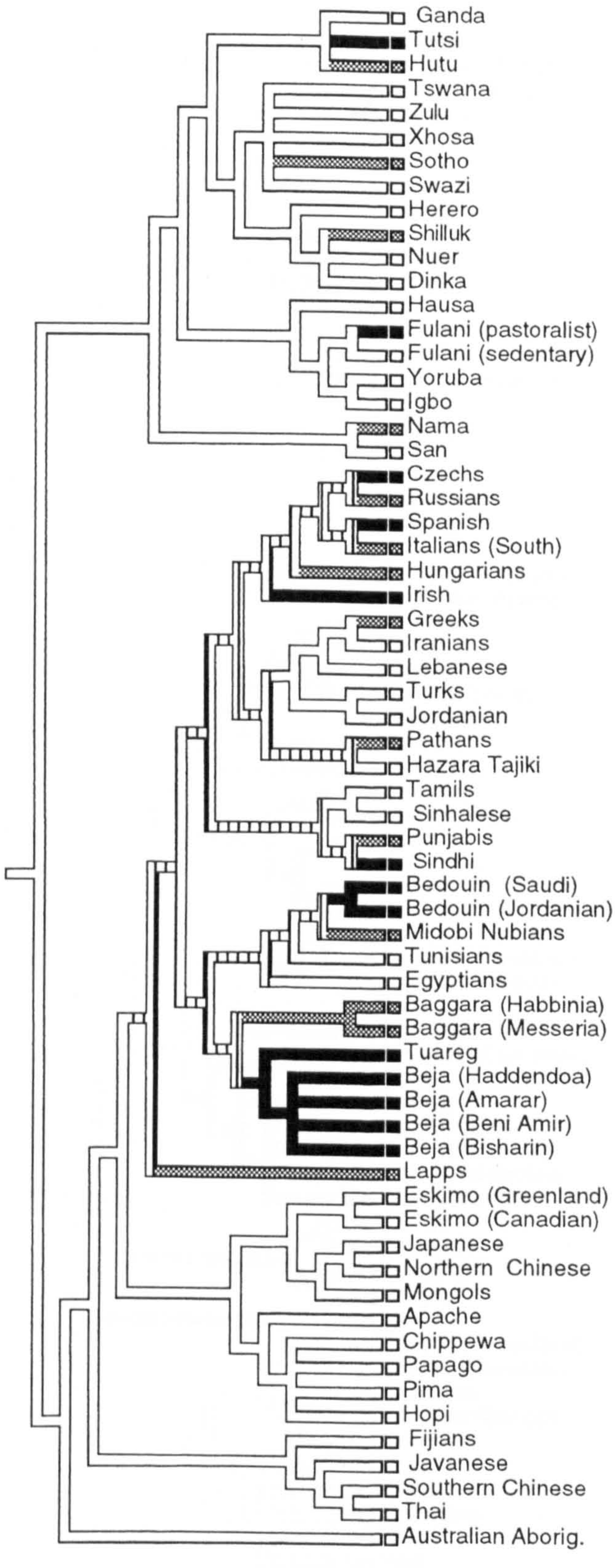


Figure 4.3 First genetic tree used in the analysis, showing lactase persistence in populations. Tree adapted from Cavalli-Sforza et al.'s (1994) F_{ST} genetic distance tree. Frequencies of lactase persistence (LP) are grouped into three groups for illustrative purposes only: black, >70% LP; grey, 30-70% LP; white, <30% LP. Ancestral states estimated using parsimony (Maddison and Maddison, 1992); hatched lines show ambiguous ancestral states.

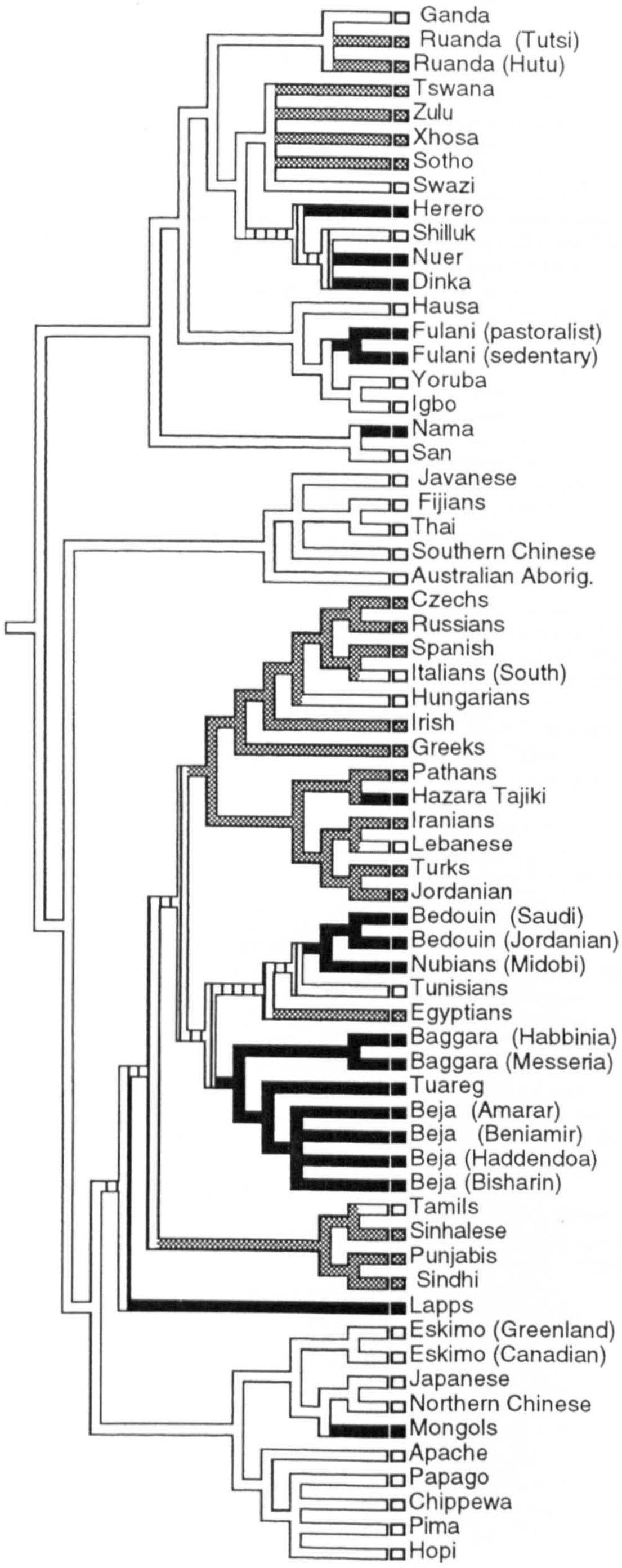


Figure 4.4 Second genetic tree used in the analysis, showing pastoralism in populations. Tree adapted from Nei genetic distance tree (Cavalli-Sforza et al., 1994). Dependence on pastoralism is grouped into three groups for illustrative purposes only: black, >50% dependence; grey, 30-50% dependence; white, <30% dependence.

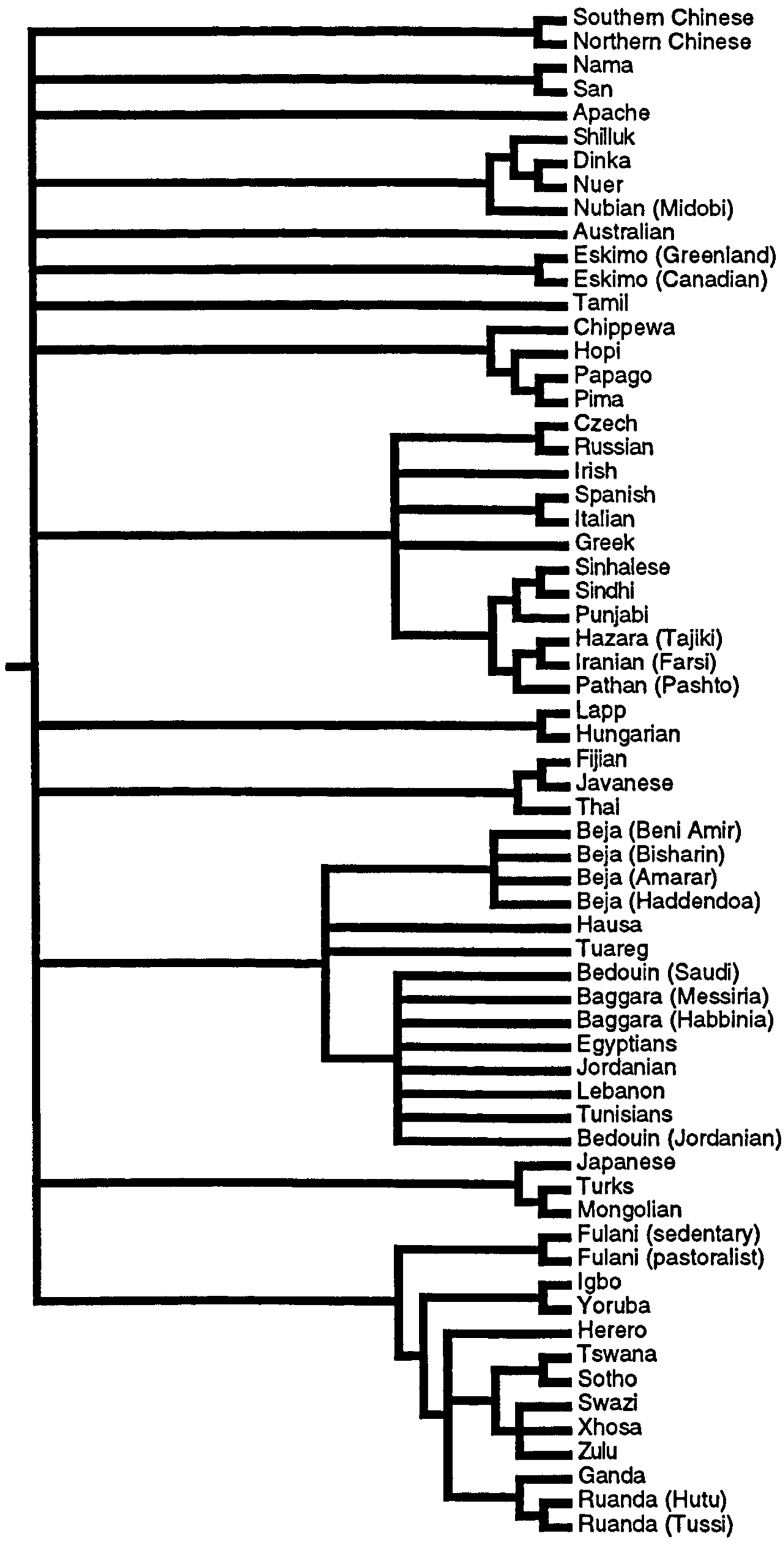


Figure 4.5 Linguistic tree used in the analysis. Adapted from Ruhlen (1991), assuming a monophyletic origin of language.

Table 4.3 Regression of contrasts in lactase persistence on pastoralism, solar intensity and aridity

Multiple regression (through the origin) results are shown. Lactase persistence was the frequency of low lactose digestion capacity in each population (hence the negative relationship with dependence on pastoralism). Significance of the slopes are t-values.

	F_{ST} genetic tree		Nei genetic tree		Language tree	
Variable	**Slope**	**Significance**	**Slope**	**Significance**	**Slope**	**Significance**
Pastoralism	-0.464	0.002	-0.456	0.002	-0.661	0.004
Solar radiation	0.113	n.s.	0.062	n.s.	-0.322	n.s.
Aridity	0.0598	n.s.	0.291	n.s.	-0.199	n.s.

Overall significance of multiple regressions

	F_{ST} genetic tree	Nei genetic tree	Language tree
Multiple R	.45	.45	.52
R^2	.20	.20	.27
Significance (F)	0.02	0.02	0.03

4.2.4 Inferring causality in the co-evolution of pastoralism and lactase persistence

Aim. The aim of this part of the analysis was to test for correlated evolution in pastoralism and HLDC using Pagel's (1994) maximum likelihood method for testing for correlated evolution among discrete traits, and to test the probable direction of character change in these variables.

Statistical methods. Pagel's (1994) method tests for correlated evolution among discrete characters, so lactose digestion capacity was divided into a high LDC/low LDC discrete variable, following its bimodal distribution in the populations in the sample (Fig. 4.6). High LDC populations are defined as having a prevalence of high LDC greater than 70 per cent. The presence or absence of milking (data from the *Ethnographic Atlas*, column 38) was used to measure pastoralism in this analysis, because it is a discrete variable. It was tested whether the independent variable, lactose digestion capacity, was more likely to change from low to high if the dependent variable, milking, was present. Milking and high LDC are shown mapped onto the phylogeny using parsimony in Figures 4.7 and 4.8.

Pagel's (1994) method requires a fully resolved tree. The tree used here was the F_{ST} genetic tree, slightly modified to create a completely resolved tree. Resolution was achieved by resolving multiple genetic nodes on linguistic relatedness where possible

(following Ruhlen, 1991). The Beja groups, and the Zulu, Ngoni and Swazi, were pooled. These groups had no variation in the relevant variables. It was assumed that all the branch lengths were equal. The tree used is shown in Figure 4.7 and 4.8.

First, the independent and the dependent models of evolutionary change in lactose digestion capacity and pastoralism were compared. In the independent model, the two characters evolve independently of one another along the branches of the tree. In the dependent model, the probability of change in one character is dependent on the state of the other.

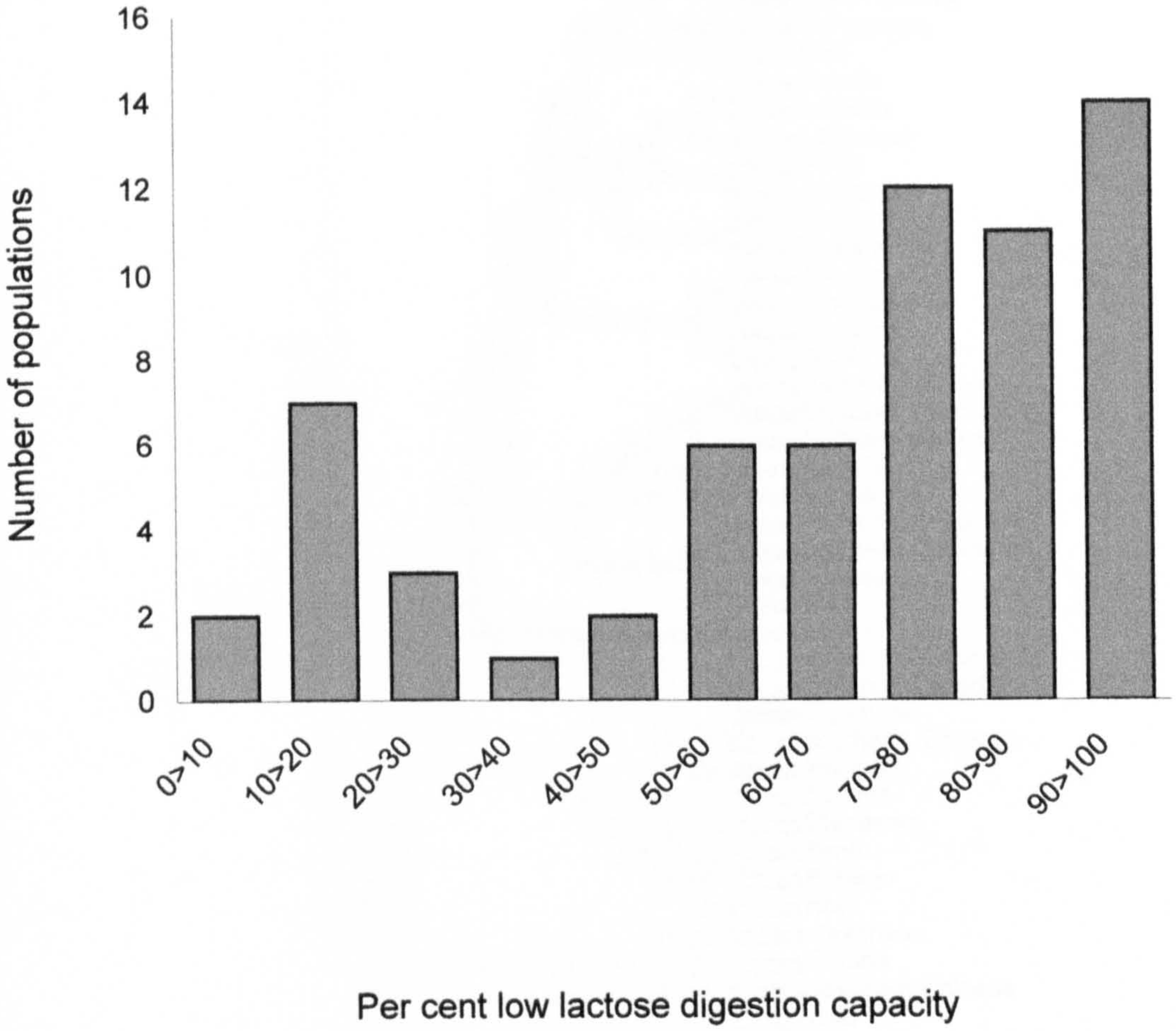
Then the probable direction of evolutionary change in the co-evolution of high LDC and milking was tested. Figure 4.9 shows a diagram of all the possible pathways of evolutionary change in these two traits. One can test which transitions were most likely, by comparing the full dependent model with a model in which the rate of one of the transitions has been set to zero. If a model where one pathway has been set to zero is much less likely to have occurred than the full model, then this pathway of evolution is likely to have been important. Conversely, if the likelihood ratios of the two models are not significantly different, then there is unlikely to have been much evolutionary change in this direction. The computer program DISCRETE was used to implement this method (Pagel, n.d.).

Results. The maximum likelihood method independent model yielded a log-likelihood of - 41.46.The model of dependent change had a log-likelihood of - 37.04. These numbers are logarithms of probabilities, and the more strongly negative numbers represent probabilities closer to zero. The dependent model is therefore

more likely. To assess whether the difference is significant, the likelihood ratio statistic is used, defined as LR = -2log[I/D] = -2[log(I) - log(D)] where I and D stand, respectively, for independent and dependent models. The program generates a probability distribution similar to a chi-square distribution, which is used to measure the significance of the LR statistic. In this case the probability that there is a relationship between the evolution of high LDC and milking, LR = 8.83, is significant at $p<0.05$. This finding corresponds with the finding from the analysis by independent contrasts that the evolution of the two traits is correlated.

The significance of each evolutionary transition is shown on Figure 4.9. From an ancestral condition of no milking (-milking) and low lactose digestion capacity (-LDC), milking (+milking) probably evolved first, followed by the evolution of high LDC (+LDC). In some cases populations with milking which evolved high LDC may have subsequently lost high LDC. It appears that high LDC never evolved without the prior presence of milking. This further supports the hypothesis that high LDC is an adaptation to dairying.

Figure 4.6 Bimodal distribution of lactose digestion capacity across populations in the sample



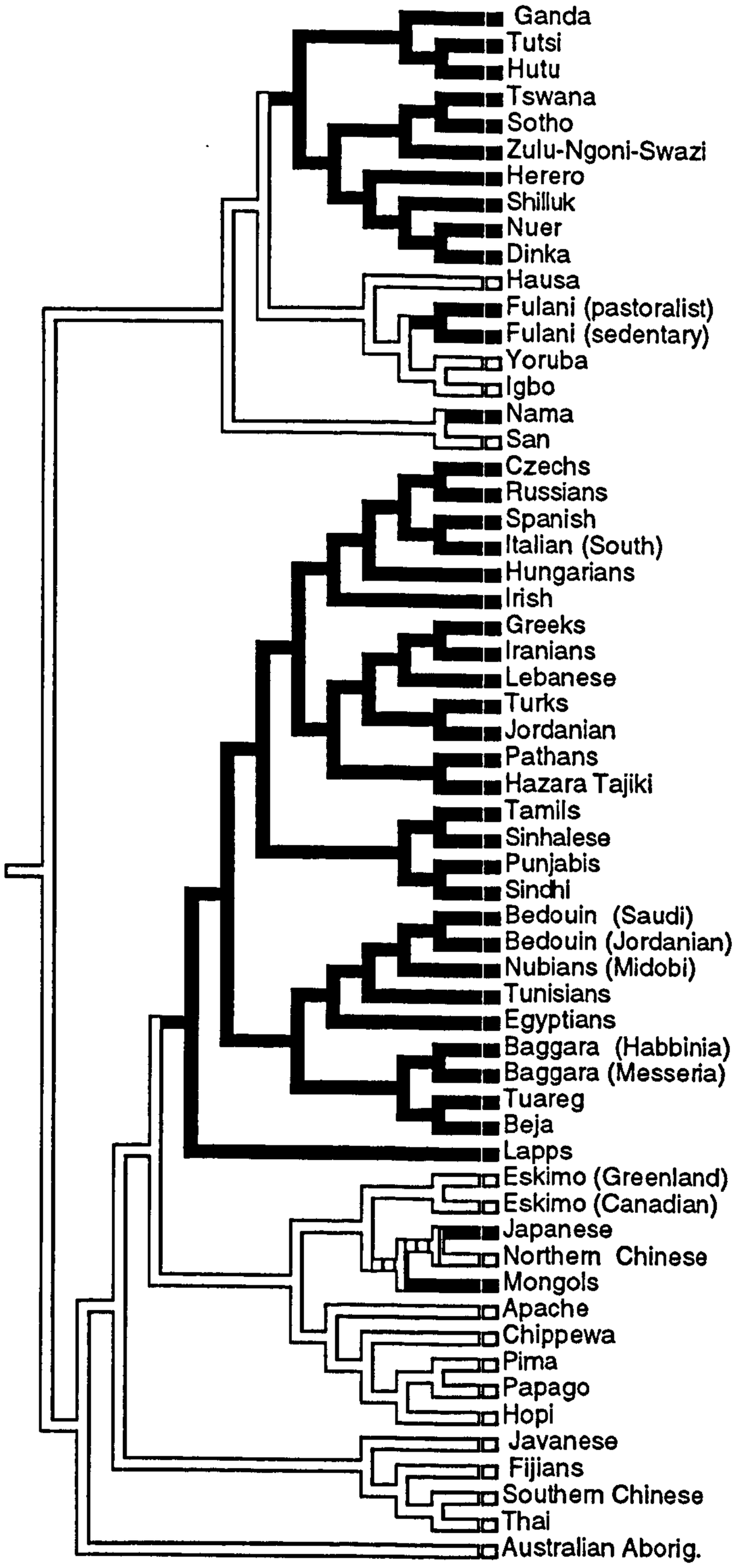


Figure 4.7 Composite tree used in the maximum likelihood analysis, showing milking. Tree is based on Cavalli-Sforza et al.'s (1994) F_{ST} distance tree. Black indicates milking populations, white indicates non-milking populations.

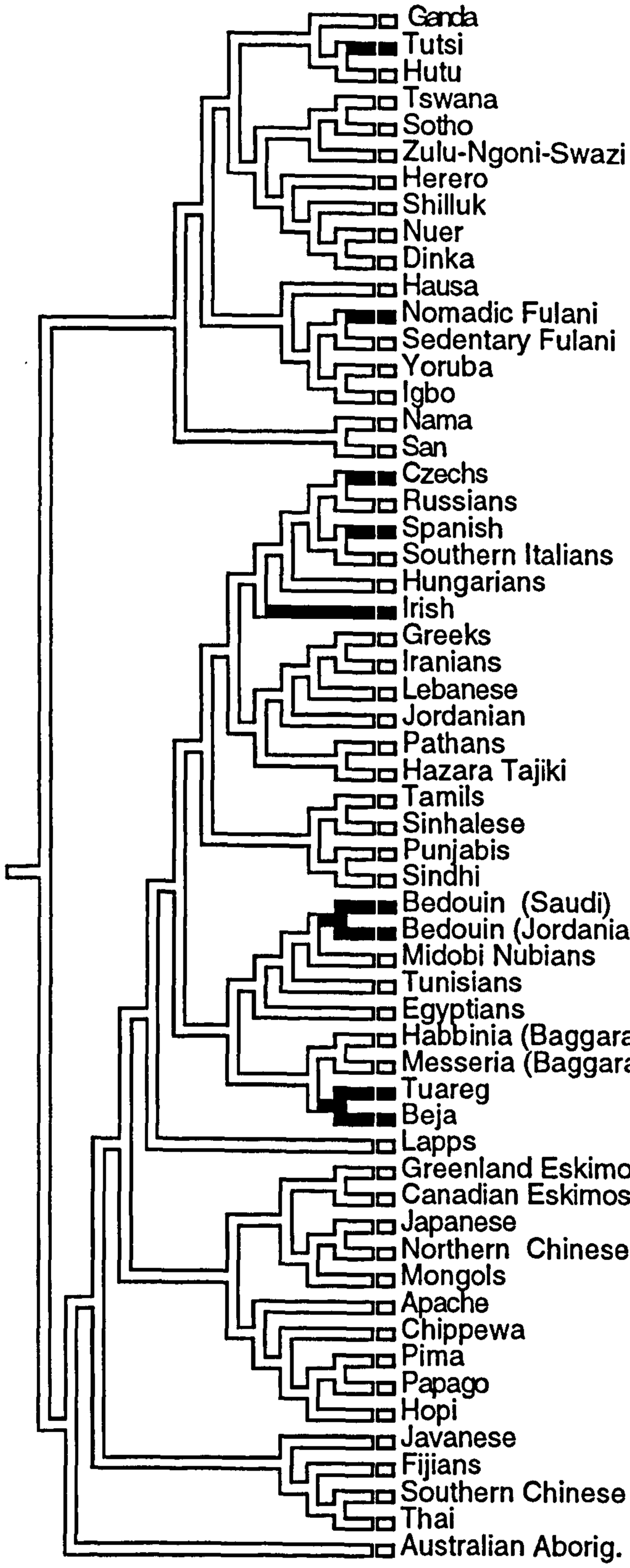
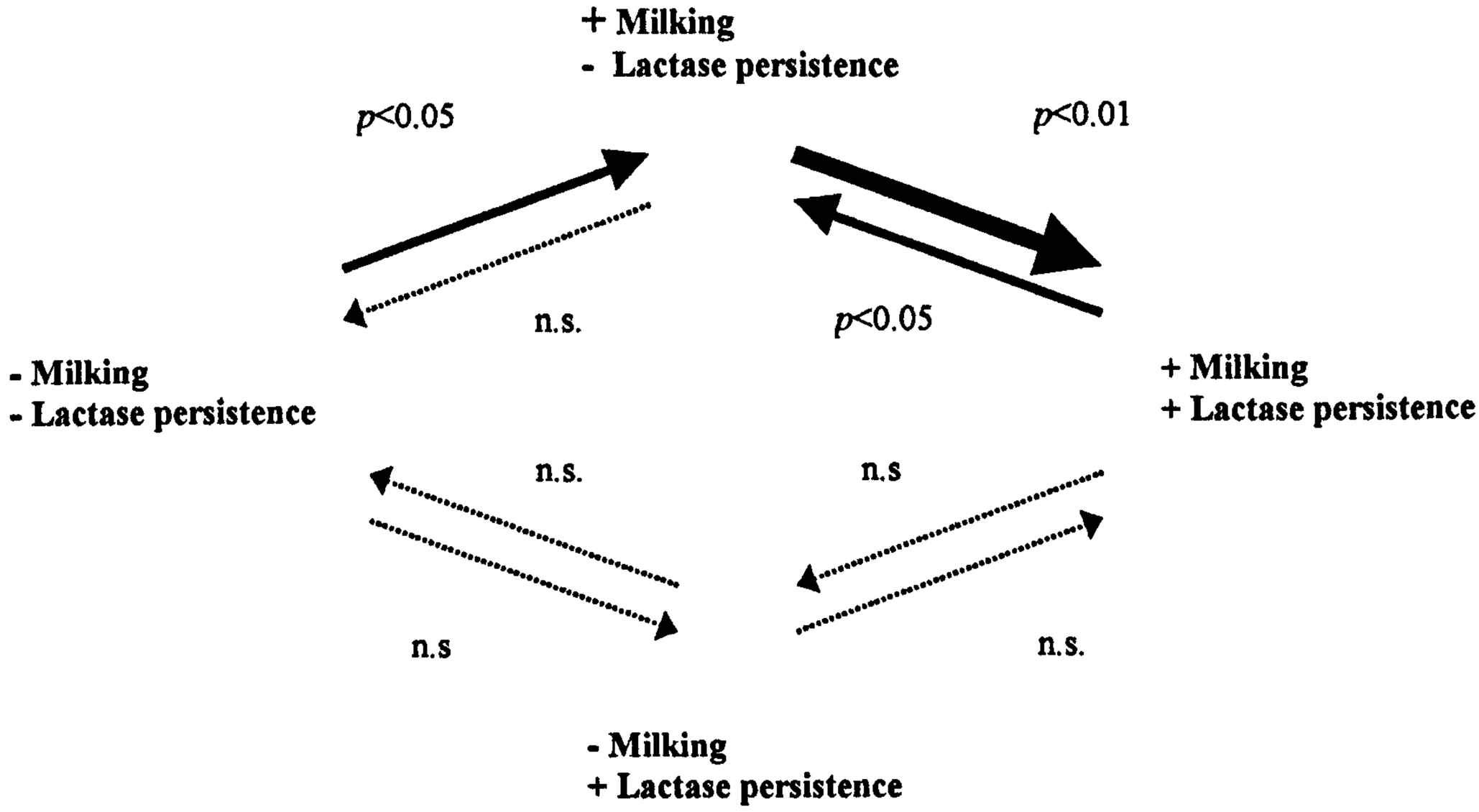


Figure 4.8 Composite tree used in the maximum likelihood analysis, showing lactase persistence (LP) in populations. Black indicates LP >70%, white indicates LP <70%.

Figure 4.9 The direction of evolutionary change in pastoralism and lactase persistence

The significance of transitions between character states are shown for a maximum likelihood model of co-evolution in pastoralism and lactase persistence. The significance of each evolutionary transition in the model is shown next to the arrows.



4.3 Conclusions and discussion

The results of the phylogenetic analysis support the hypothesis that adult lactose digestion capacity evolves in populations which rely on domestic livestock in their subsistence. The results do not support Flatz and Rotthauwe's (1973) hypothesis that fresh milk consumption and high LDC are additionally selected for at high latitudes with limited sunlight, or Cook and Al-Torki's (1975) hypothesis that high LDC is additionally selected for in hot, arid environments. Aridity and pastoralism are related, because pastoralism is often adopted as a means of subsistence in regions where rainfall is too low for agriculture, but no evidence was found here that aridity *per se* provides an additional selective pressure for the evolution of high LDC. The analysis using Pagel's (1994) maximum likelihood model shows that the evolution of high LDC is strongly associated with the presence of pastoralism, and further shows that pastoralism is always adopted before high LDC evolves.

A phylogenetic perspective on the evolution of lactase persistence provides an explanation for why some pastoralists, for example the Herero in southern Africa, have a low prevalence of lactase persistence. These populations may have become pastoralists too recently for the gene for lactase persistence to have spread. The archaeological evidence suggests that pastoralism in southern Africa dates from the 1st millennium AD (Sherratt, 1980; Bower, 1995). This is much more recent than pastoralism in north Africa and the Middle East, where pastoralists with a high

prevalence of lactase persistence live (for example, the Bedouin and the Tuareg). Other questions remain unanswered, for example, why lactase persistence is rare in some Sudan-Sahel populations (e.g. the Nuer and Dinka) in a region with an ancient pastoralist tradition. Gene flow from non-pastoralist populations may have occurred, or these populations may be relatively recent immigrants to the region.

It may appear surprising that low solar intensity (at high latitudes) is not an additional selective pressure for the evolution of high LDC, given that in northern Europe high LDC is prevalent, yet domestic animals only represent about 30% of total subsistence in these regions today (Murdock, 1967). Pastoralists with similar levels of lactase persistence in Africa and the Middle East have much higher levels of dependence on animals. Archaeological evidence of subsistence practices in northern Europe in the Neolithic may shed some light on this apparent discrepancy. Liden (1995) carried out a dietary study of two Swedish Neolithic populations using nitrogen and carbon isotopes in Neolithic skeletons. She found that the Neolithic populations were pastoralists, rather than (as previously thought) mixed farmers relying heavily on cereals, like modern northern Europeans. If the ancestors of modern northern Europeans were pastoralists, this could explain the prevalence of high LDC in northern Europe today. This is assuming that a high meat diet also indicates that milk was consumed, which may not have been the case. Sherratt (1981) argued that the 'secondary products revolution' involving milk and wool production post-dated the origin of domesticated animals by several thousand years.

It is not surprising that contemporary levels of reliance on pastoralism have changed since the Neolithic period in Europe. What is perhaps surprising is that reliance on

pastoralism has been sufficiently stable worldwide, over millennia, for contemporary ethnographic evidence to have explanatory power over an evolutionary process that began thousands of years ago, selection for lactase persistence in adults. The analysis of the transmission between populations of the traits related to lactase persistence (section 4.2.2) suggests that pastoralism may be a highly conserved trait down the generations. Pastoralism may therefore be stable enough for the evolution of high LDC to have occurred, and for this evolutionary effect still to be detectable in extant populations.

Chapter 5

The sociobiology of wealth inheritance in Africa[9]

5.0 Summary

Inheritance practices, and the cultural traits hypothesised to be associated with them, are shown to be inherited from 'mother' to 'daughter' populations. Phylogenetic comparative methods were used to control for non-independence among populations, while testing sociobiological predictions about the socio-ecological correlates of matrilineal and patrilineal inheritance, in a cross-cultural African sample. Patriliny was found to be associated with pastoralism and polygyny. Matriliny was negatively associated with pastoralism and polygyny. Patriliny is usually adopted after the adoption of cattle, and patriliny and pastoralism occurring together is a stable state.

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[9] An earlier version of this analysis was published in: Mace R, Holden C. 1999. Evolutionary ecology and cross-cultural comparison: the case of matrilineal descent in sub-Saharan Africa. In Lee PC (ed). Comparative Primate Socioecology. Cambridge University Press, Cambridge, p387-405.

The direction of male altruism to kin was associated with paternity confidence: increasing altruism towards uterine kin was associated with a decrease in paternity confidence. The results are consistent with sociobiological predictions.

5.1 Inheritance in Africa

Wealth inheritance practices are highly variable across cultures. There is evidence that people transmit wealth adaptively, in ways which maximise their inclusive fitness. Relatedness, age, sex and birth order all affect wealth inheritance. Their effects vary, within and across cultures, depending on environmental variables such as mode of subsistence and socio-economic status (Hartung, 1982; Crook and Crook, 1988; Borgerhoff Mulder, 1988; Gaulin and Boster, 1990; Mace, 1996). In this chapter, evolutionary predictions about sex bias in wealth inheritance were tested, in a cross-cultural sample of African cultures.

The majority of African cultures have patrilineal or matrilineal inheritance; both patrilineal and matrilineal features are present in many African cultures, but one type of inheritance usually predominates (e.g. Harris and Harris, 1964; Rigby, 1969; Goody, 1969). Under both patrilineal and matrilineal inheritance, different types of property are usually transmitted between individuals of the same sex (Murdock, 1949; Goody, 1976). In matrilineal societies, wealth is transmitted through females (uterine

relatives) (Richards, 1950; Radcliff-Brown, 1952; Schneider and Gough, 1961). Men's property (or 'male' wealth) is transmitted from the mother's brother to the sister's son (Fox, 1967; Flinn, 1981; Hartung, 1985). It may also be inherited from older to younger brothers, before passing from the eldest brother to his sister's son (Murdock, 1967). 'Female' property is inherited from mother to daughter (Sear, 1998).

In patrilineal societies, property is transmitted through males (agnatic relatives), usually from father to son (Fox, 1967). Again wealth may be inherited from older to younger brothers before being inherited by the eldest brother's son. This is common in patrilineal West African cultures (Murdock, 1967). Hartung (1981) noted that inheritance to brothers is partly matrilineal, in that full brothers are related through their mother as well as their father. If there is no son, wealth is inherited by more distant agnatic relatives. Ethnographic evidence on the transmission of female property in patrilineal societies is often lacking (e.g. Murdock, 1967). Presumably it is mostly passed from mother to daughter, as in matrilineal societies, but most productive resources are owned by men.

In some cultures (mostly in North Africa) the distinction between male and female property is not as strictly marked, and wealth may be transmitted to children of either or both sexes, often with sons receiving more than daughters. Daughters may inherit if they have no brothers, or they may receive a smaller inheritance than sons (Murdock, 1967; Goody, 1976). Some cultures have no fixed rules about inheritance, mostly hunter-gatherers with little valuable property. Many nomadic pastoralists also have no inheritance rules for land because they do not individually own land (Murdock, 1967).

The geographical distribution of matrilineal and patrilineal inheritance in 138 African cultures is shown on a map in Figures 5.1 and 5.2. The inheritance of movable property (which includes livestock) is shown in Figure 5.1. The inheritance of land is shown in Figure 5.2. Matrilineal cultures are clustered in a 'matrilineal belt' (Richards, 1950) in central Africa, and are also found in west and North Africa. A 'patrilineal belt' extends from east to west, immediately north of matrilineal central Africa. A cluster of patrilineal cultures is also found in southeast Africa. Son-biased inheritance predominates among sedentary Arabs and Bedouin in North Africa. The aim of this analysis was to account for this variation.

Figure 5.1 Inheritance of movable property in Africa

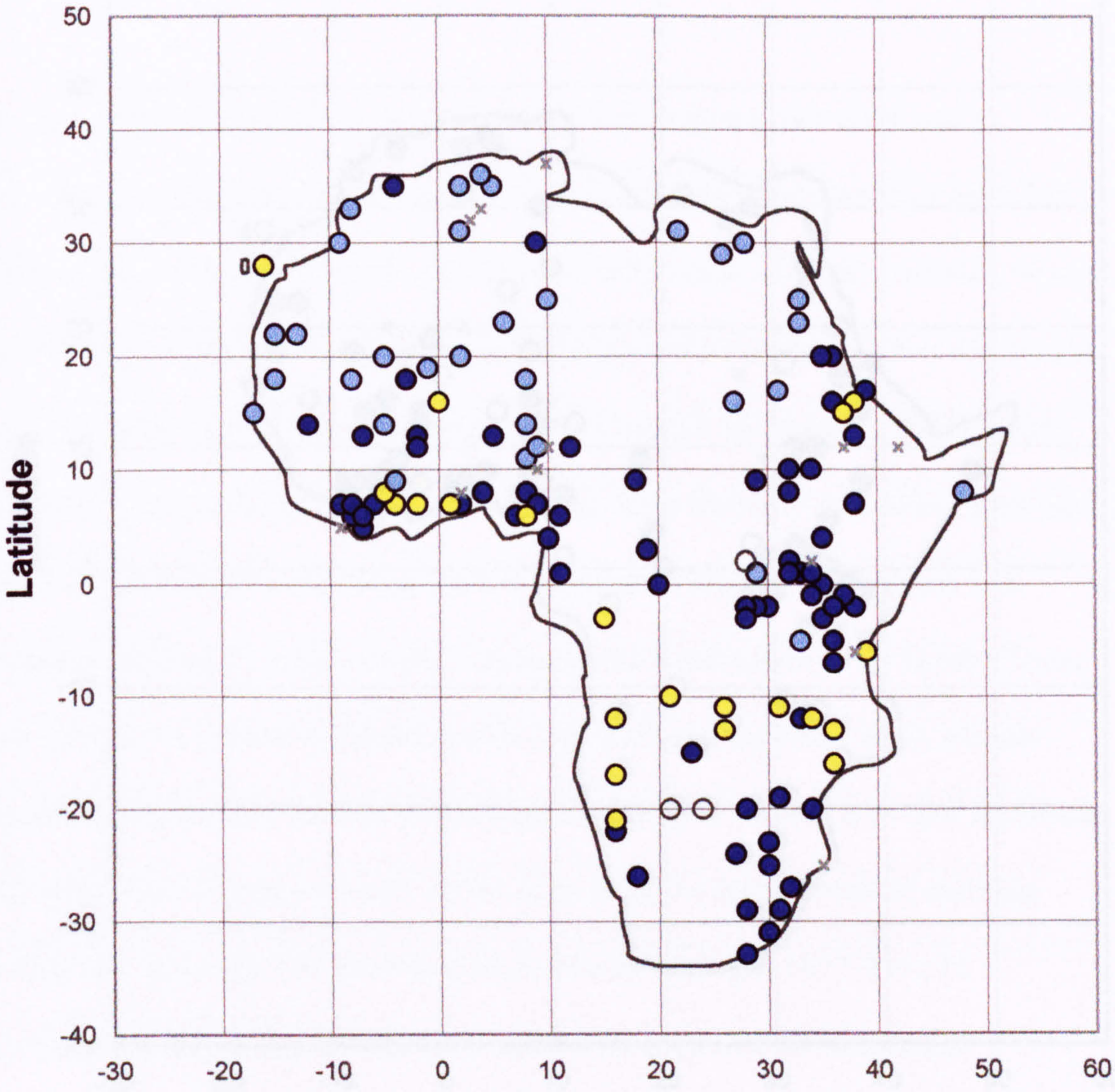
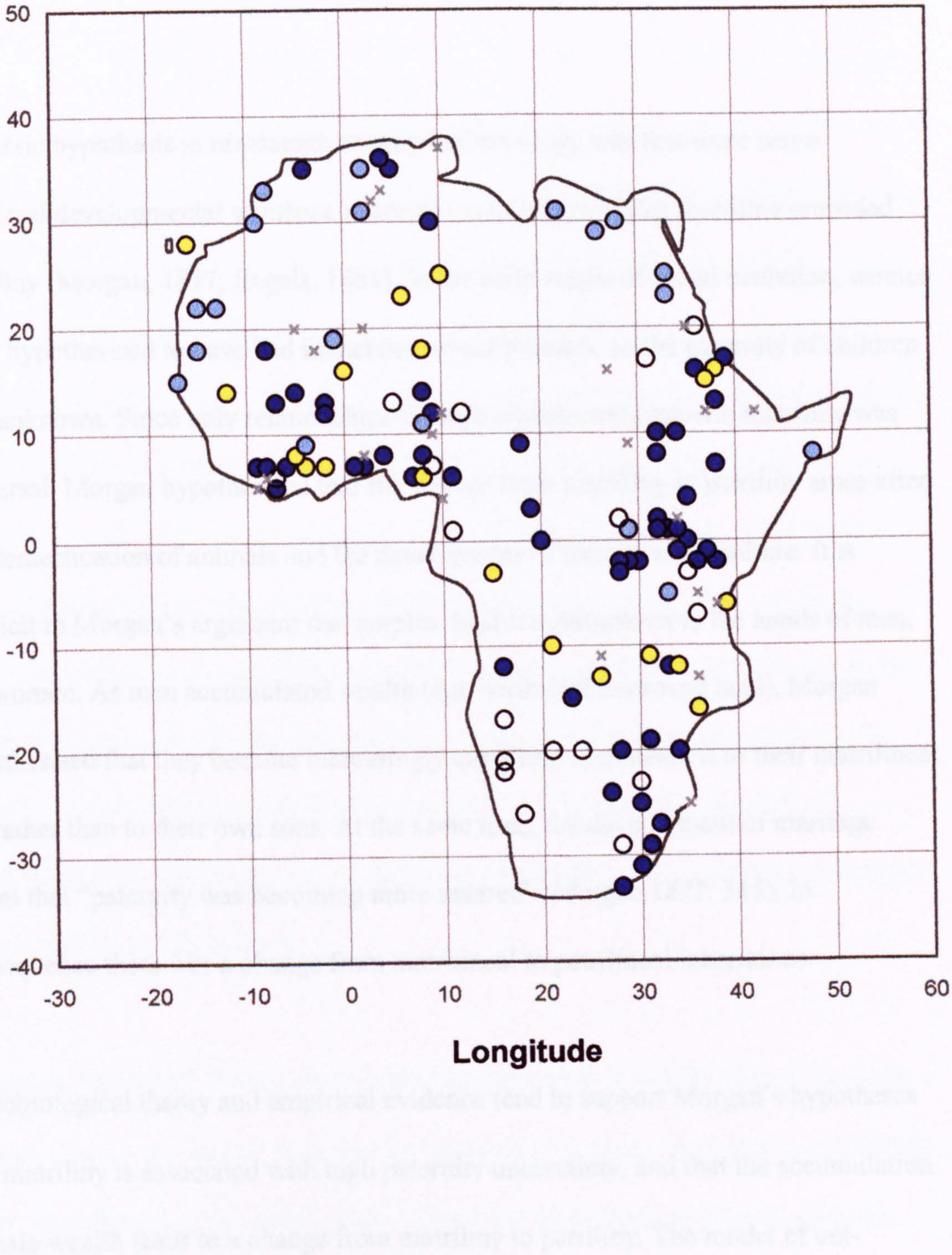


Figure 5.2 Inheritance of land in Africa



5.2 Hypotheses for variation in inheritance

A classic hypothesis in nineteenth century anthropology was that there was a universal developmental sequence in social evolution, in which matriliny preceded patriliny (Morgan, 1877; Engels, 1884). In the early stages of social evolution, women were hypothesised to have had numerous sexual partners, so the paternity of children was unknown. Since only relationships through women were known, matriliny was universal. Morgan hypothesised that the change from matriliny to patriliny arose after the domestication of animals and the development of intensive agriculture. It is implicit in Morgan's argument that surplus wealth accumulates in the hands of men, not women. As men accumulated wealth (e.g. herds and improved land), Morgan hypothesised that they became increasingly unwilling to transmit it to their matrilineal kin rather than to their own sons. At the same time, the development of marriage meant that "paternity was becoming more assured" (Morgan 1877: 345). In consequence there was a change from matrilineal to patrilineal inheritance.

Sociobiological theory and empirical evidence tend to support Morgan's hypotheses that matriliny is associated with high paternity uncertainty, and that the accumulation of male wealth leads to a change from matriliny to patriliny. The model of uni-directional social evolution is not accepted in contemporary evolutionary theory; however, evidence that African cultures which gain cattle become patrilineal, and that patriliny plus cattle is a stable state, is presented in section 5.3.4 (see Figure 5.13).

5.2.1 Pastoralism, polygyny and patrilineal inheritance

Pastoralism. Aberle (1961) investigated the relationship between livestock and descent rules in a cross-cultural sample of 565 cultures (Murdock's *World Ethnographic Sample*, Murdock, 1957). He found a highly significant negative correlation between matriliny and pastoralism in Africa. He also noted that across the world matriliny is most common in horticultural regions (defining horticulture as agriculture without the plough). Matriliny is generally absent in regions with plough agriculture and pastoralism. Aberle (1961: 680) concluded that, "The cow is the enemy of matriliny, and the friend of patriliny". Mace and Holden (1999) found that patriliny was associated with pastoralism, in a phylogenetic comparative analysis, using two cross-cultural samples of 89 and 227 sub-Saharan African cultures. Pastoralism was also found to be associated with patriliny, and negatively associated with matriliny, in this chapter.

Polygyny. Murdock (1949) hypothesised that those factors which increase the status of men, relative to women, including the presence of movable property such as herds or slaves, polygyny and warfare, lead to patrilocal residence and descent. Descent (determining group membership) is highly correlated with wealth inheritance. Polygyny was also found to be associated with patriliny, and negatively associated with matriliny, in this chapter.

A sociobiological interpretation of the association between pastoralism, polygyny and son-biased or patrilineal inheritance. Wealth inheritance is a form of parental investment, defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Wealth is finite, so wealth given to one child is no longer available for other children. Evolutionary theory predicts that parents will discriminate among their offspring in ways which maximise their (the parent's) inclusive fitness. If male reproductive success is more strongly associated with inherited wealth than female reproductive success, then it is adaptive for parents to transmit more wealth to sons than daughters (Trivers and Willard, 1973; Maynard Smith, 1980). This is the case in most African pastoralist cultures, where men can use livestock to pay bridewealth to marry polygynously. Livestock often also need to be defended against raiders, done by men rather than women (Mace, 1996). From an evolutionary perspective, the presence of herds, slaves and possibly warfare (hypothesised to be associated with patriliny by Murdock, 1949) are signs of high variance in male wealth, which would be expected to lead to polygyny (Orians, 1969; see chapter 6).

If the benefits of inherited wealth to males are sufficiently greater than the benefits to females, then in the absence of sons it is adaptive to transmit wealth to more distant male relatives (e.g. nephews) rather than daughters. This gives rise to fully patrilineal inheritance, as opposed to simply son-biased inheritance (Hartung, 1982a). In this case, the additional benefit of wealth inheritance to a male heir (e.g. a nephew) relative to a daughter would be expected to compensate for the male heir's lower degree of relatedness.

Valuable property is therefore usually inherited patrilineally. This includes livestock, especially cattle and camels. If land becomes valuable, i.e. if the productivity of land is increased by use of the plough or irrigation and if land becomes scarce, then it is also expected to be transmitted to sons. A change from matrilineal to son-biased inheritance has occurred in a number of societies with increasing wealth and inequality among men. Examples are reviewed in Douglas (1969) and include the Lodogaba in West Africa (Goody, 1962), Gold Coast cocoa-farmers (Hill, 1963), the Plateau Tonga in southeast Africa (Colson, 1958) and Mwinilunga cash-crop farmers (Turner, 1957).

5.2.2 The paternity uncertainty hypothesis

From an evolutionary perspective, matriliny represents a puzzle, because men in matrilineal societies transmit wealth to their sisters' sons, rather than to their own sons. Inclusive fitness theory predicts that if the costs and benefits of an altruistic act are constant, then individuals should direct their altruism towards relatives who are as closely related as possible, e.g. offspring and siblings (Hamilton, 1964). Matrilineal inheritance is thus puzzling, because men appear to be transmitting wealth towards nephews, to whom they are only half as related (r=0.25 in the case of full nephews) as men are to their own sons (r=0.5).

The paternity uncertainty hypothesis for matrilineal inheritance states that if paternity uncertainty is high, then men may be on average more closely related to their sisters' children than to their wives' children, so it is adaptive for men to transmit wealth to their sisters' children rather than their own putative children (Alexander, 1974; Greene, 1978; Flinn, 1981; Hartung, 1981; 1985). As noted above, a functional relationship between matriliny and paternity confidence was hypothesised by Morgan (1877). Other early statements of the paternity uncertainty hypothesis are reviewed by Hartung (1985).

Evidence for an association between matriliny and paternity uncertainty. Many cross-cultural studies have found a correlation between matriliny and low paternity certainty. Using data from the Human Area Relations Files, Flinn (1981) found a highly significant association between high paternity confidence and altruism towards agnatic kin (relatives through males), and between low paternity confidence and altruism towards uterine kin (relatives through females) in a sample of 288 societies. He deliberately over-represented matrilineal cultures in the sample, because their actual frequency in the world is low. His sample is therefore particularly vulnerable to the criticism that the cultures in it are not independent. Matriliny tends to be clustered in certain regions so it is likely that matrilineal cultures from these regions share many similarities due to their common ancestry, including perhaps their level of paternity confidence. The relationship between matriliny and paternity confidence among the African cultures in Flinn's (1981) dataset was therefore re-analysed here, using independent contrasts to control for non-independence among populations. Male altruism towards uterine kin was found to be highly correlated with low

paternity certainty, and altruism towards agnatic kin with high paternity certainty, confirming Flinn's (1981) original results (see section 5.3.5).

Other studies which have found evidence for a cross-cultural correlation between matriliny and high paternity uncertainty include Gaulin and Schlegel (1980), Hartung (1981) and Hartung (1985). Wolfe and Gray (1980) and Gray and Wolfe (1982; c.f. Hartung, 1982b) have criticised aspects of Gaulin and Schlegel's (1980) and Hartung's (1981) methods, but taken together, these studies provide strong evidence that matrilineal cultures tend to have lower levels of paternity confidence than patrilineal cultures.

However, matriliny does not seem to be an adaptive male strategy, even in societies with relatively high paternity uncertainty. Paternity uncertainty needs to be extremely high before a man is, on average, more related to his sister's children than to his wife's children. Greene (1978) showed that the probability of paternity, p, must be less than 0.268 before a man is more related to his sister's children than to his own putative children. (This calculation takes into account the probability that a man has a different father to his sister if paternity uncertainty is high). Hartung (1981; 1985) showed that over several generations a man's probabilistic relationship to his patrilineal descendants decreases geometrically, as p is multiplied each generation. If $p<0.725$ then a man's probabilistic relationship to his great grandson is lower than his probabilistic relationship to his third generation matrilineal heir. If $p<0.46$ then a man's cumulative relationship to six or more generations of his sister's sons is higher than his cumulative relationship to six or more generations of his own sons. He suggested that matrilineal inheritance might be an adaptive long-term male strategy if

$p<0.46$, although it was unclear why the short-term strategy of investing in sons, with higher short-term benefits, would not invade the population. Levels of paternity probability less than 0.268 or 0.46 are lower than observed levels of paternity certainty in most matrilineal societies. It is likely that low paternity certainty is a consequence, rather than a cause, of matriliny. The costs of non-paternity for men are lower in matrilineal societies than in patrilineal societies, so parents and husbands may invest less effort in ensuring the chastity of their daughters and wives.

Is matriliny a female strategy? Hartung (1985) hypothesised that matriliny is a female strategy. He showed that matrilineal inheritance is an adaptive grand-maternal strategy at any level of paternity certainty less than 1.0. Under matrilineal inheritance, wealth is transmitted from the grandmother's brother to her son, and then to her daughter's son. This is an adaptive grand-maternal strategy because daughters' children have a higher probabilistic relatedness to the grandmother than sons' children.

But in most societies men control most productive resources and have authority over women, so how can a grand-maternal strategy arise and persist if it has costs for fathers? One possible explanation is that women's status and control over productive resources are relatively high in matrilineal societies (Poewe, 1978; Mandala, 1990; Lovett, 1997; Peters, 1997). Evidence of high female status and control over resources, especially land, is found in ethnographies of many African matrilineal societies. For example, in the Tonga in Malawi, Lovett (1997) wrote that 'As a member of her matrilineage...an adult Lakeside Tonga woman could claim certain economic rights, undoubtedly the most important of which was independent

control over her land'. In Luapula in Zambia, Poewe (1978) wrote that 'matriliny enables women to control the land, collect remittances from children, and divorce "useless" husbands'.

A second possible explanation for matrilineal inheritance, despite its costs for fathers, is that paternity uncertainty may promote altruism towards uterine kin, at the expense of agnatic kin, within the extended family. This could be a secondary factor explaining matriliny. Gaulin et al. (1997) found that in modern America, matrilineal aunts and uncles invest significantly more in their nieces and nephews than patrilineal aunts and uncles (both types of aunt invested more than either type of uncle). Paternity uncertainty also appears to affect grandparental care. Euler and Weitzel (1996) found that in modern Germany maternal grandmothers provided the most care, followed by maternal grandfathers, paternal grandmothers and paternal grandfathers respectively. They reported similar patterns for adoption by grandparents in a number of cultures worldwide, including the Inuit, the East Pacific Rotumans, and the Trobriand Islanders. Men have a higher probabilistic relationship to their sisters' children than to their brothers' children, so brothers may exert pressure on one another to invest in their mutual sisters' children (Flinn 1981). Hartung (1985) suggested that once matriliny is instituted, men have a vested interest in maintaining it in some capacities – for example, as brothers and sister's sons who inherit wealth from their male matrilineal kin.

Inheritance by daughters. Until now we have been considering inheritance of 'male' property, which in matrilineal societies is transmitted from the mother's brother to the sister's son. All previous sociobiological studies of matriliny have focussed on the

inheritance of male wealth, perhaps assuming that women never own important resources (e.g. Flinn, 1981; Gaulin and Schlegel, 1981; Hartung, 1981; 1985). However, inheritance to daughters does exist. Murdock (1967) recorded three North American cultures with female ownership of land, with mother to daughter inheritance, the Arikira, the Hidatsa and the Mandan. Murdock also noted that in the Zuni "a man's land is inherited by his daughters" – presumably the man's land came originally from his wife. Many ethnographies of matrilineal societies have focussed on political rights, such as succession to the status of Headman (e.g. Richards, 1950; Radcliff-Brown, 1952; Schneider and Gough, 1961). It is possible that political functions were transmitted from the mother's brother to the sister's son, while effective control over land passed from mothers to daughters, but has not been given similar prominence in the literature. Inheritance of land by daughters is the norm in parts of central Africa today, for example among the Chewa in Malawi (Sear, 1998). Female control of land is also documented in matrilineal societies in Zambia, in the Kaonde (Crehan, 1997) and, as noted above, in Luapula (Poewe, 1978). Poewe (1978) and Crehan (1997) did not specify whether daughters inherit land from their mothers in the Kaonde and in Luapula. Daughters inherit a portion of land in the Taita in southern Kenya (Harris and Harris, 1964).

Inheritance to daughters provides a simple explanation for how matriliny might arise. For property that belongs to women, inheritance to daughters and daughters' children is adaptive for both the mother and father – there is no conflict between the sexes. If the benefits of inherited wealth for males and females are similar, then inheritance to daughters' children (and subsequent heirs through females) is adaptive for both the grandmother and the grandfather. Both men and women have a higher probability of

relationship to their descendants through females (e.g. their daughters' children) than to descendants through males (e.g. their sons' children). This is shown in Table 5.1. All probabilistic relationships through males are lower than relationships through females, because relatedness through men is multiplied by *p*, the probability of paternity, which is less than 1.0.

We may therefore hypothesise that matrilineal inheritance arises from inheritance to daughters, in cultures which distinguish between male and female property, and in which female property is more economically important than male property (c.f. Murdock, 1949). We may ask why women own important resources such as land in some cultures, for example the Chewa in Malawi (Sear, 1998). Mace and Holden (1999) suggested that in some societies where daughters inherit land, sons may be pursuing a 'roving male' reproductive strategy, seeking promiscuous mating opportunities, leaving women to support their own children. This may be an adaptive male strategy when land is poor, so it is not worth defending or cultivating by males. In the North American Hidatsa, Arikira and Mandan, where daughters inherited land from their mothers, men's main subsistence activities were hunting and fishing, and farming was an exclusively female activity (Murdock 1949; 1967).

Table 5.1 Men's and women's relatedness (*r*) to male and female descendants

GRANDFATHER		**GRANDMOTHER**	
Own children		**Own children**	
r=0.5*p*		**r=0.5**	
Sons' children	**Daughters' children**	**Sons' children**	**Daughters' children**
r=(0.5*p*)(0.5*p*)	**r=(0.5*p*)(0.5)**	**r=(0.5)(0.5*p*)**	**r=(0.5)(0.5)**
=0.25p^2	**=0.25*p***	**=0.25*p***	**=0.25**

5.2.3 The relationship between the hypotheses

The two main evolutionary hypotheses for sex biased inheritance are:

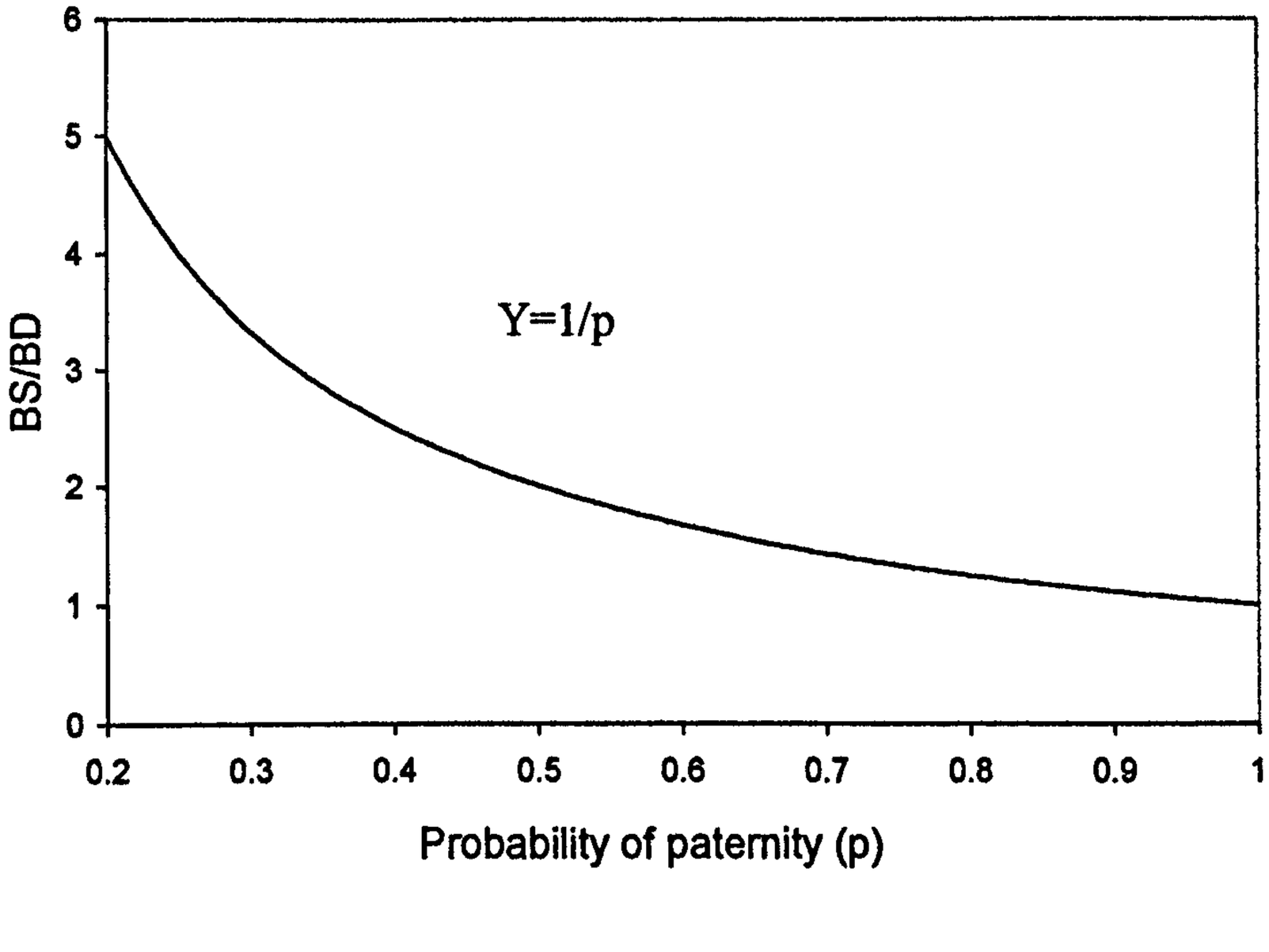
1. Wealth inheritance to sons is adaptive if the benefits of wealth are greater for sons than daughters.
2. Wealth inheritance to daughters' children is adaptive if the risk of non-paternity for sons' children is high.

These two hypotheses are related. One would expect parents to pass their wealth on to sons if the benefit to sons of inheriting wealth, multiplied by the probability of non-paternity of a son's putative children, is greater than the benefit to daughters of

inheriting wealth. Otherwise parents should pass inherited wealth to their daughters. For example, if p=0.5 then the benefit of inherited wealth to sons must be more than twice the benefit to daughters, for it to be adaptive to transmit wealth to sons (p is the probability of paternity). This is shown graphically in Figure 5.3. Inheritance to daughters is expected to occur in cases where the property concerned is not valuable enough to enable sons to marry polygynously, or where sons are unable to use inherited wealth to marry polygynously, for example if monogamy was the only permitted type of marriage. Full patriliny (where more distant male relatives rather than daughters inherit in the absence of sons) is expected if the benefit to the male of inherited wealth, multiplied by p, multiplied by the male relative's lower relatedness (r), is greater than the benefit of inherited wealth to a daughter.

Figure 5.3 Sex biased grandparental investment

The vertical axis shows the ratio of the benefit of inherited wealth to sons (BS) and daughters (BD). The horizontal axis shows the probability of paternity. The line Y = 1/p shows when it is equally adaptive to invest in sons' and daughters' children At values above this line it is adaptive for to invest in sons and their male children. For values below this line it is adaptive to invest in daughters' children and descendants through the female line.



5.3 Methods and results

The hypotheses were tested on a cross-cultural African sample. The analysis was limited to Africa because, despite its cultural diversity, the variables hypothesised to be associated with different inheritance practices are comparable across the continent. In most African societies men can use wealth to marry polygynously. Livestock are an important type of wealth in Africa., whereas under horticultural agriculture, prevalent in Africa, land is not very productive or valuable (c.f. Douglas, 1969). This contrasts with other continents. In North America before 1492 there were no large domestic livestock. In many parts of Eurasia, polygyny is illegal. Land is also more productive, scarcer and more valuable than in most of Africa. Plough agriculture and irrigation (rare in the African sample used here) are widespread in Eurasia (Goody, 1976). Livestock are therefore not such a good indicator of male wealth.

5.3.1 Data and trees

A sample of 138 African cultures was used to investigate the transmission, between populations, of inheritance practices, pastoralism and polygyny (section 5.3.2), and to test the relationship between these variables (section 5.3.3). The sample includes all those African cultures found in the *Ethnographic Atlas* (Murdock, 1967, and

instalments of *Ethnology*, 1962-7) which are also found in Cavalli-Sforza et al.'s (1994) *History and Geography of Human Genes*, and Ruhlen's (1991) *Classification of the world's languages*. Some language synonyms were found in Voeghlin and Voeghlin (1977). The resulting sample is shown in Table 5.2.

The *Ethnographic Atlas* includes data on the inheritance of land and movable property (columns 74 and 76, Murdock, 1967). Movable property includes livestock, which is often the most valuable type of wealth among pastoralists and agro-pastoralists. Inheritance rules for land and movable property in each culture are shown in Table 5.2. Many cultures really have mixed inheritance systems – for example, even in patrilineal cultures one or two cattle may be transmitted from the mother's brother to the sister's son (e.g. in the Gogo in Tanzania, Rigby, 1969). However, matrilineal and patrilineal inheritance had to be treated as discrete categories here because more detailed data on inheritance were lacking for most cultures.

Dependence on livestock as a percentage of total subsistence in each culture is estimated in Murdock's (1967) *Ethnographic Atlas* (column 10). Murdock's codes were adapted for use here as shown in Table 5.3. Data on polygyny were also from the *Ethnographic Atlas* (column 14). In the *Ethnographic Atlas* cultures are classified as monogamous, occasionally polygynous (less than 20% of marriages polygynous) and generally polygynous (more than 20% of marriages polygynous). Monogamy was given a score of zero, occasional polygyny was scored 1 and general polygyny was scored 2. Dependence on pastoralism and polygyny in cultures in the sample are shown in Table 5.2.

Table 5.2 Inheritance, pastoralism and polygyny in 138 African cultures

Cultures' names and code in Murdock's (1967) Ethnographic Atlas (EA) are shown. Per cent dependence on pastoralism, level of polygyny (0=none, 1=0-20% of marriages, 2=>20% marriages), and inheritance rules for land and movable property are shown.

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Afar	Ca6	80	2	Missing data	Missing data
Afikpo Ibo	Af23	10	2	Mixed, mainly matrilineal	Mixed, mainly matrilineal[10]
Ahaggaren	Cc9	50	0	Matrilineal	Children, mostly sons
Algerians	Cd12	30	1	Children, mostly sons	Children, mostly sons
Amarar	Ca35	90	1	No rule	Patrilineal, formerly matrilineal[11]
Ambo	Ab19	30	2	No rule	Matrilineal
Amhara	Ca7	30	0	Patrilineal	Patrilineal
Antessar	Cc5	60	0	Missing data	Patrilineal
Anyi	Af39	10	2	Matrilineal	Matrilineal
Asben	Cc10	50	1	Matrilineal	Children, mostly sons
Ashanti	Af3	0	2	Matrilineal	Matrilineal
Aulliminden	Cc8	60	0	.	Missing data
Azjer	Cc11	50	0	Matrilineal	Children, either sex or both
Bakwe	Af46	10	2	Patrilineal	Patrilineal
Bambara	Ag1	20	2	Patrilineal	Patrilineal
Bamum	Ae50	10	2	Patrilineal	Patrilineal
Basa	Ah11	20	2	Patrilineal	Patrilineal

[10]Counted as matrilineal
[11]Counted as patrilineal

Table 5.2 (cont.)

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Barea	Ca32	20	2	Matrilineal	Matrilineal
Bashi	Ae13	40	2	Patrilineal	Patrilineal
Baule	Af9	10	2	Matrilineal	Matrilineal
Bemba	Ac3	0	2	Matrilineal	Matrilineal
Berabish	Cc7	90	1	Missing data	Children, mostly sons
Bergdama	Aa4	20	2	No rule	Patrilineal
Bete	Af7	10	2	No rule	Patrilineal
Bira	Ae30	10	2	Children, either sex or both	Children, either sex or both
Bisharin	Ca5	80	1	Missing data	Patrilineal
Bogo	Ca37	90	1	Patrilineal	Patrilineal
Bororo	Cb8	80	2	No rule	Patrilineal
Bozo	Ag7	0	2	Patrilineal	Children, mostly sons
Bwaka	Ai23	10	2	Patrilineal	Patrilineal
Chaamba	Cc16	70	2	Missing data	Missing data
Chokwe	Ac12	10	1	Matrilineal	Matrilineal
Chopi	Ab22	20	0	Missing data	Missing data
Delim	Cc17	50	1	Children, mostly sons	Children, mostly sons
Dinka	Aj11	50	2	Missing data	Patrilineal
Diula	Ag27	10	2	Children, mostly sons	Children, mostly sons
Duala	Ae12	10	2	Missing data	Patrilineal
Egyptians	Cd2	30	1	Children, mostly sons	Children, mostly sons
Ewe	Af36	10	2	Patrilineal	Matrilineal
Falasha	Ca31	30	0	Missing data	Missing data
Fang	Ae3	10	2	No rule	Patrilineal

Table 5.2 (cont.)

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Fon	Af1	20	2	Patrilineal	Patrilineal
Gagu	Af51	10	2	Patrilineal	Patrilineal
Ganda	Ad7	10	2	Patrilineal	Patrilineal
Gisu	Ad9	20	2	Patrilineal	Patrilineal
Gogo	Ad24	40	2	No rule	Patrilineal
Guanche	Cd11	20	0	Matrilineal	Matrilineal
Hadza	Aa9	0	1	No rule	Patrilineal
Hamama	Cd13	70	2	Patrilineal	Patrilineal
Hamyan	Cd14	70	1	Children, mostly sons	Children, mostly sons
Herero	Ab1	60	2	No rule	Matrilineal
Hunde	Ae15	30	2	Patrilineal	Patrilineal
Ibo	Af10	10	2	Patrilineal	Patrilineal
Ifora	Cc12	50	0	Missing data	Children, mostly sons
Kababish	Cc6	80	2	No rule	Children, mostly sons
Kabyle	Cd4	30	1	Patrilineal	Children, mostly sons
Kamba	Ad34	30	2	Patrilineal	Patrilineal
Kanawa	Cb9	20	2	Patrilineal	Children, mostly sons
Kaonde	Ac32	0	2	Matrilineal	Matrilineal
Karamajong	Aj30	60	2	Missing data	Missing data
Kenuzi	Cd1	30	1	De	Children, mostly sons
Kikuyu	Ad4	30	2	Patrilineal	Patrilineal
Kpelle	Af15	10	2	Patrilineal	Patrilineal
Kran	Af47	10	2	Missing data	Patrilineal
Kru	Af48	10	2	Missing data	Missing data
Kunama	Ca33	20	1	Matrilineal	Matrilineal

Table 5.2 (cont.)

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Kunda	Ac37	0	2	Matrilineal	Matrilineal
Kung	Aa1	0	1	No rule	No rule
Kunta	Cc18	60	0	Children, mostly sons	Children, mostly sons
Kurama	Ah21	20	2	Missing data	Missing data
Lakeshore Tonga	Ac13	10	1	Matrilineal	Matrilineal
Lozi	Ab3	20	2	Patrilineal	Patrilineal
Luo	Aj6	20	2	Patrilineal	Patrilineal
Maasai	Aj2	90	2	Patrilineal	Patrilineal
Maguzawa	Cb1	20	2	Missing data	Missing data
Mbundu	Ab5	20	2	Patrilineal	Matrilineal
Mbuti	Aa5	0	1	No rule	No rule
Meban	Ai45	20	2	Patrilineal	Patrilineal
Meru	Ad35	30	2	Patrilineal	Patrilineal
Midobi	Cb11	90	2	Missing data	Matrilineal (changing to 'children, mostly sons')[12]
Mongo	Ae4	0	2	Patrilineal	Patrilineal
Moroccans	Cd16	30	1	Children, mostly sons	Children, mostly sons
Mossi	Ag47	20	2	Patrilineal	Patrilineal
Mzab	Cc4	10	0	Missing data	Missing data
Nama	Aa3	50	1	No rule	Patrilineal
Naron	Aa7	0	1	No rule	No rule
Ndau	Ab17	20	2	Patrilineal	Patrilineal
Ndebele	Ab9	40	2	Patrilineal	Patrilineal
Ndembu	Ac6	10	2	Missing data	Matrilineal
Ngere	Af56	20	2	Patrilineal	Patrilineal
Ngoni	Ac9	10	2	Patrilineal	Patrilineal

[12]Midobi Nubians were classified as neither matrilineal nor patrilineal.

Table 5.2 (cont.)

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Ngulu	Ad51	10	1	Missing data	Missing data
Nuer	Aj3	50	2	Patrilineal	Patrilineal
Nyamwezi	Ad20	10	2	Mixed patrilineal and matrilineal	Mixed patrilineal and matrilineal
Nyanja	Ac38	10	2	Matrilineal	Matrilineal
Nyoro	Ad2	20	2	Patrilineal	Patrilineal
Pedi	Ab15	30	2	Patrilineal	Patrilineal
Pondo	Ab10	50	2	Patrilineal	Patrilineal
Rega	Ae17	10	2	Patrilineal	Patrilineal
Regeibat	Cc1	70	1	Children, mostly sons	Children, mostly sons
Riffians	Cd3	30	1	Patrilineal	Patrilineal
Ruanda	Ae10	30	2	Patrilineal	Patrilineal
Saadi	Cd18	60	1	Children, mostly sons	Children, mostly sons
Sandawe	Aa6	20	1	Missing data	Patrilineal
Sanusi	Cd20	60	2	Children, mostly sons	Children, mostly sons
Sara	Ai22	30	2	Patrilineal	Patrilineal
Serer	Ag22	20	2	Matrilineal	Patrilineal (matrilineal until recently)[13]
Shilluk	Ai6	20	2	Patrilineal	Patrilineal
Shluh	Cd5	30	0	Children, mostly sons	Children, mostly sons
Shona	Ab18	20	2	Patrilineal	Patrilineal
Sidamo	Ca16	30	2	Patrilineal	Patrilineal
Siwans	Cc3	30	1	Children, mostly sons	Children, mostly sons
Soga	Ad46	20	2	Patrilineal	Patrilineal
Somali	Ca2	90	2	Children, mostly sons	Children, mostly sons

[13]Counted as patrilineal

Table 5.2 (cont.)

Culture name	Code in EA	Pastoralism (%)	Polygyny	Inheritance of land	Inheritance of movables
Sotho	Ab8	30	2	No rule	Patrilineal
Swazi	Ab2	20	2	Patrilineal	Patrilineal
Tazarawa	Cb25	30	2	Patrilineal	Inheritance to children (either sex or both)
Teke	Ac19	10	0	Matrilineal	Matrilineal
Tigre	Ca38	80	1	Patrilineal	Patrilineal
Tiv	Ah3	10	2	No rule	Patrilineal
Trarza	Cc19	60	0	Children, mostly sons	Children, mostly sons
Tswana	Ab13	40	2	Patrilineal	Patrilineal
Tumbuka	Ac36	10	2	Patrilineal	Patrilineal
Tunisians	Cd21	20	1	Missing data	Missing data
Turkana	Aj5	30	2	Patrilineal	Patrilineal
Udalan	Cc13	20	0	Matrilineal	Matrilineal
Ulad nail	Cd17	70	1	Patrilineal	Children, mostly sons
Venda	Ab6	20	2	No rule	Patrilineal
Wodaabe	Cb24	90	2	No rule	Patrilineal
Wolof	Cb2	30	2	Children, mostly sons	Children, mostly sons
Xhosa	Ab11	30	2	Patrilineal	Patrilineal
Yao	Ac7	10	1	Missing data	Matrilineal
Yatenga	Ag2	20	2	Patrilineal	Patrilineal
Yoruba	Af6	10	2	Patrilineal	Patrilineal
Zazzagwa	Cb26	30	2	Children, mostly sons	Children, mostly sons
Zenaga	Cc20	70	0	Patrilineal	Children, mostly sons
Zigula	Ad28	20	2	Matrilineal	Matrilineal
Zulu	Ab12	40	2	Patrilineal	Patrilineal

Table 5.3 Adaptation of the *Ethnographic Atlas* codes on reliance on pastoralism

Murdock's (1967) code	Estimated per cent reliance on pastoralism
0 (=0-5% dependence)	0
1 (=6-15% dependence)	10
2 (=16-25% dependence)	20
3 (=26-35% dependence)	30
4 (=36-45% dependence)	40
5 (=46-55% dependence)	50
6 (=56-65% dependence)	60
7 (=66-75% dependence)	70
8 (=76-85% dependence)	80
9 (=86-100% dependence)	90

Trees. Two trees were used as models of the past relationships among the populations in the sample. The first tree was a linguistic tree, adapted from Ruhlen (1991), shown in Figures 5.4-5.7. The second tree was a genetic tree, adapted from Cavalli-Sforza et al.'s (1994: Fig. 3.5.1) African F_{ST} genetic distance tree, shown in Figure 5.8. Many nodes on the genetic tree are not resolved, especially among Bantu-speaking cultures. This has the effect of reducing the sample size in a phylogenetic comparative analysis.

In Figure 5.4, inheritance of movable property has been mapped onto the linguistic tree using parsimony, using MacClade (Maddison and Maddison, 1992). Inheritance of land is shown on the tree in Figure 5.5. The root of Niger-Kordofanian speakers is patrilineal, but several apparently independent instances of matriliny occur, especially among Bantu-speaking cultures. A few cases of matrilineal inheritance occur in North Africa, especially in the Tuareg (mostly for land rather than livestock). Matriliny tends to be clustered within small groups of closely related populations. Dependence on pastoralism is shown on the tree in Figure 5.6, divided into three levels (0-20%, 30-50% and 60-100% dependent) for illustrative purposes. Niger-Kordofanian speakers mostly have low levels of dependence on livestock, with the exception of the Fulani and Herero. Many highly pastoralist cultures are found in the Nilotic and Afro-Asiatic language groups. Marriage practices have been mapped onto the tree in Figure 5.7. A contrast between high levels of polygyny within the Niger-Kordofanian and Nilotic language groups, and lower levels of polygyny among Afro-Asiatic and Khoisan cultures, can be seen.

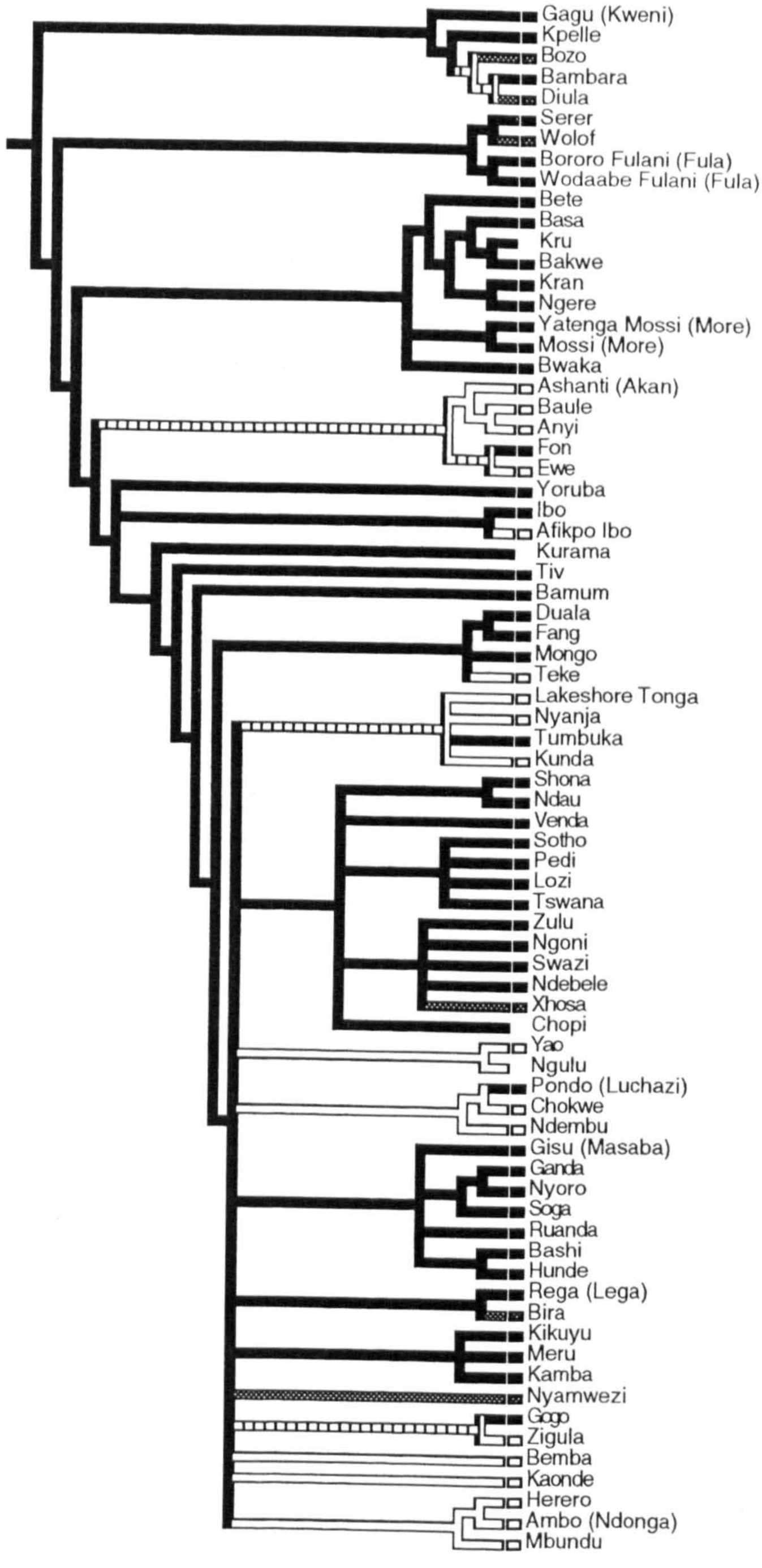


Figure 5.4A Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Niger-Kordofanian language phylum is shown, with inheritance of movable property (including livestock) mapped onto the tree. Black=patriliny, white=matriliny, dark grey=other inheritance rules.

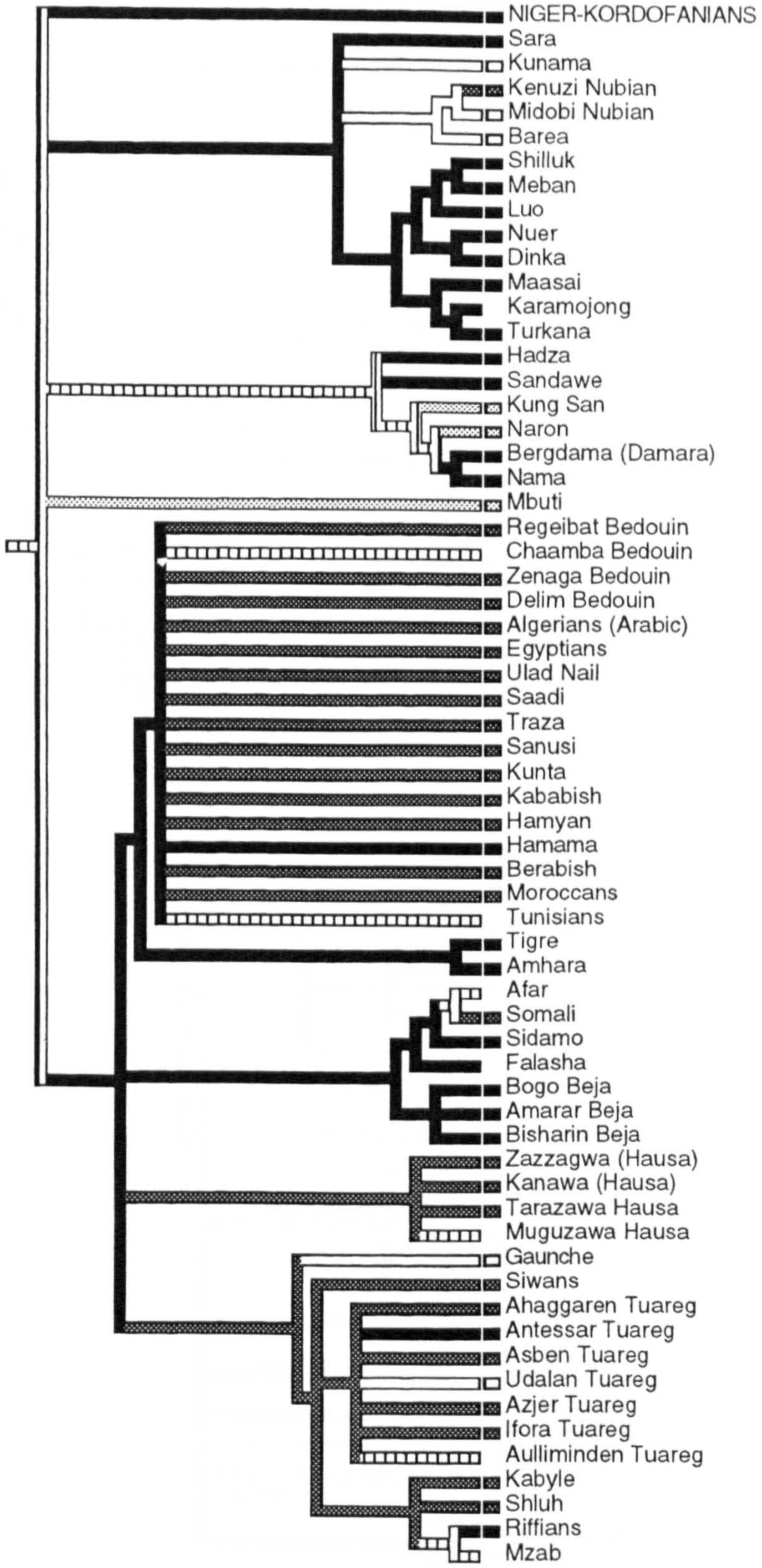


Figure 5.4B Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Mbuti (original language unknown), Afro-Asiatic, Nilo-Saharan and Khoisan language phyla are shown, with inheritance of movable property (including livestock) mapped onto the tree. Black=patriliny, white=matriliny, dark grey=other inheritance rule (mostly 'to children, mostly sons'), light grey=no inheritance rule.

Figure 5.5A Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Niger-Kordofanian language phylum is shown, with inheritance of land mapped onto the tree. Black=patriliny, white=matriliny, dark grey=other inheritance rule, light grey=no inheritance rule.

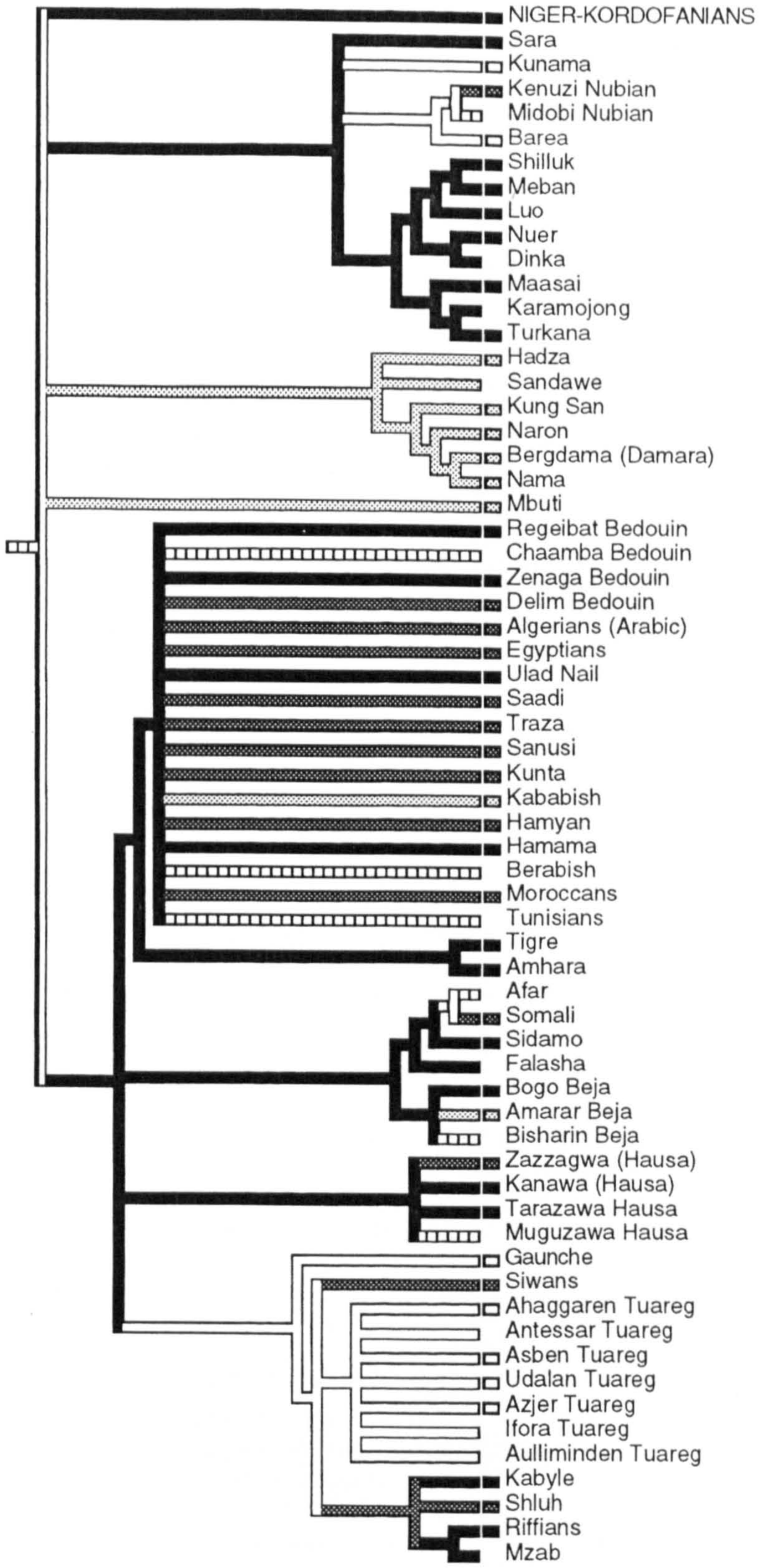


Figure 5.5B Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Mbuti (original language unknown), Afro-Asiatic, Nilo-Saharan and Khoisan language phyla are shown, with inheritance of land mapped onto the tree. Black=patriliny, white=matriliny, dark grey=other inheritance rule (mostly 'to children, mostly sons'), light grey=no inheritance rule.

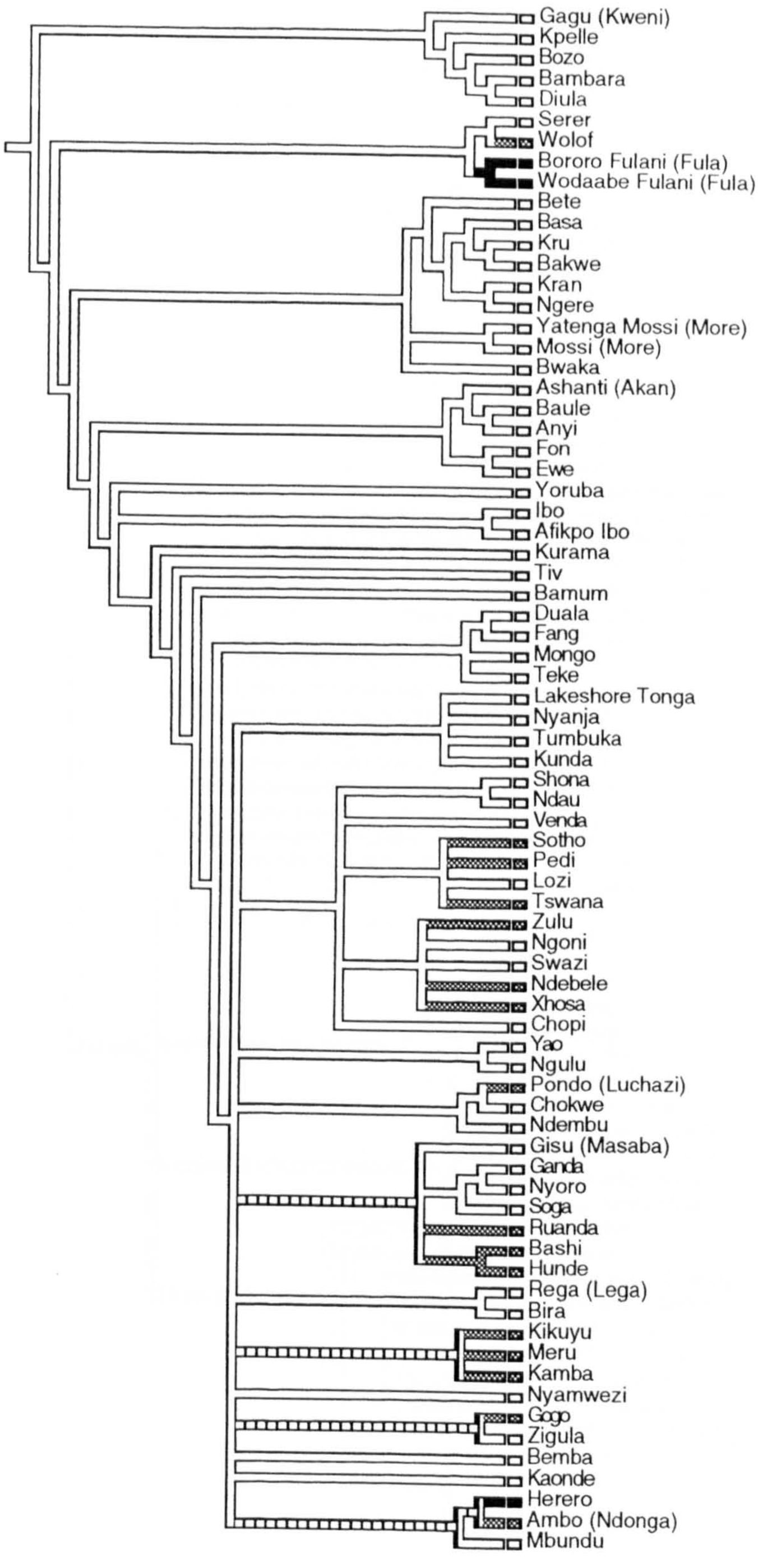


Figure 5.6A Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Niger-Kordofanian language phylum is shown, with pastoralism mapped onto the tree, grouped into three categories for illustrative purposes. White=0-20% pastoralist, grey=30-50% pastoralist, black=60-100% pastoralist.

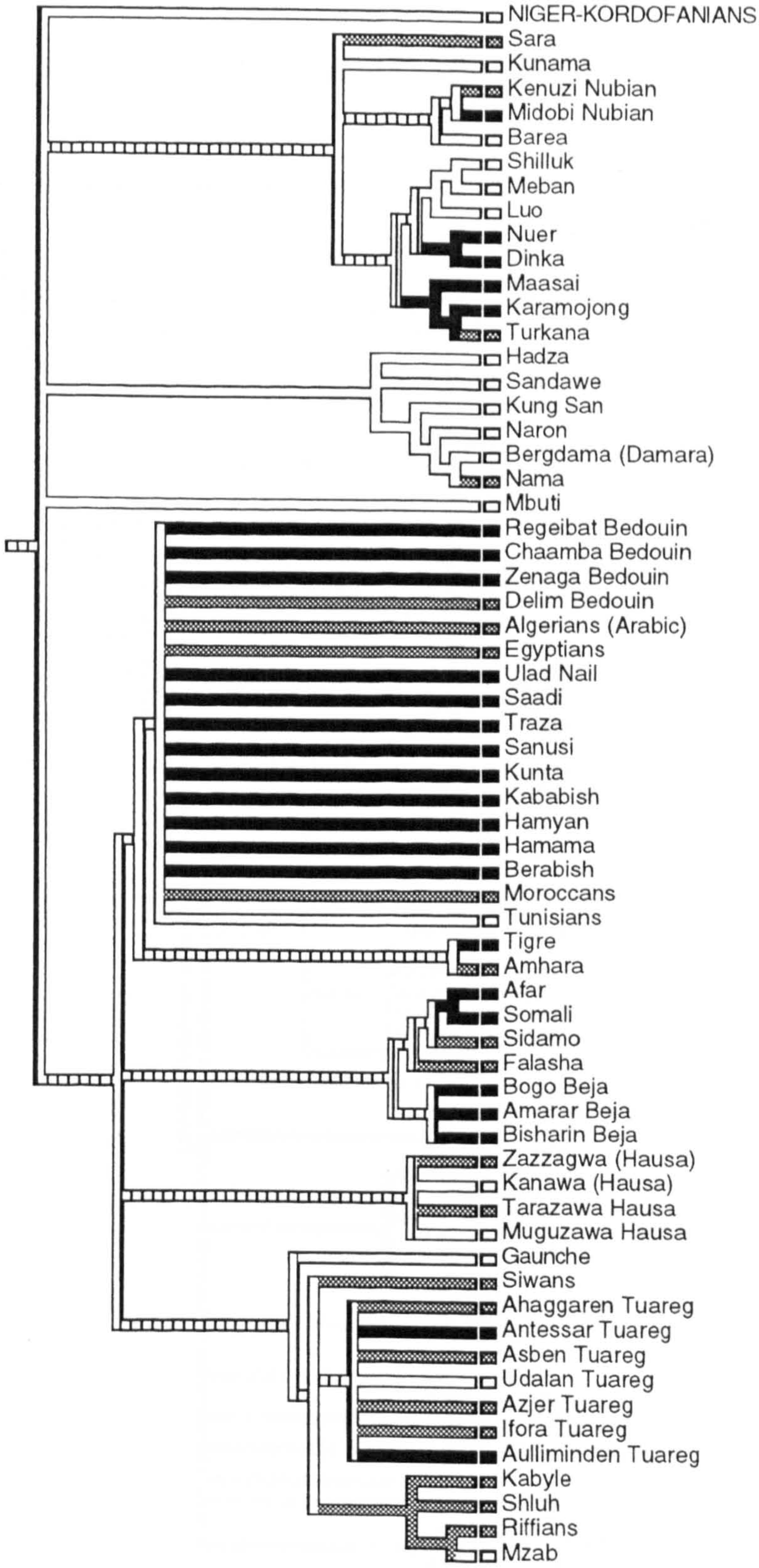


Figure 5.5B Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Mbuti (original language unknown), Afro-Asiatic, Nilo-Saharan and Khoisan language phyla are shown, with pastoralism mapped onto the tree, grouped into three categories for illustrative purposes. White=0-20% pastoralist, grey=30-50% pastoralist, black=60-100% pastoralist.

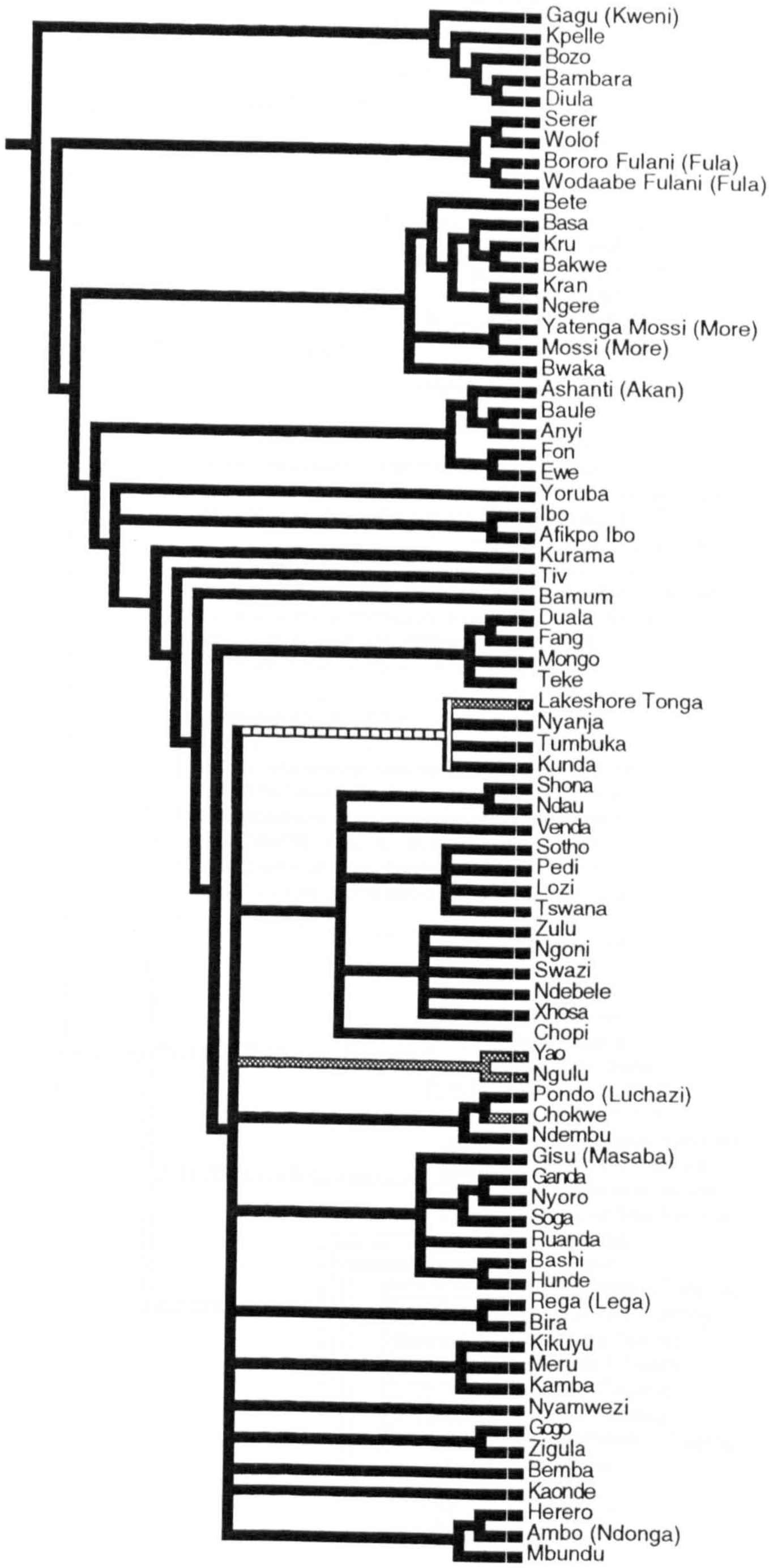


Figure 5.7A Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Niger-Kordofanian language phylum is shown, with the level of polygyny mapped onto the tree. Black=general polygyny (>20% of marriages), grey=occasional polygyny (<20% of marriages are polygynous).

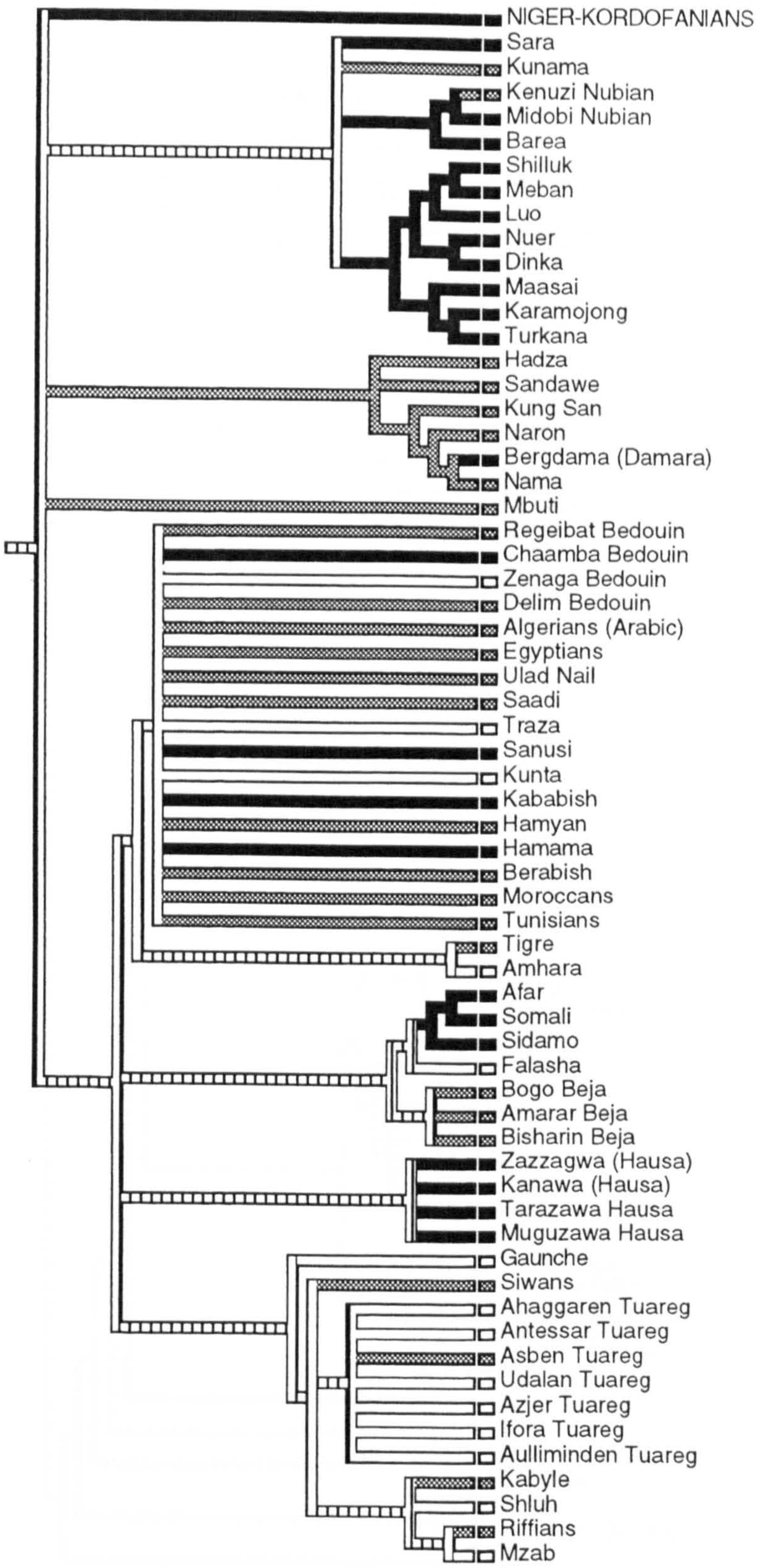


Figure 5.5B Linguistic tree of Africa, adapted from Ruhlen (1991), shown over two pages. On this page, the Mbuti (original language unknown), Afro-Asiatic, Nilo-Saharan and Khoisan language phyla are shown, with the level of polygyny mapped onto the tree. Black=general polygyny (>20% of marriages), grey=occasional polygyny (<20% of marriages are polygynous), white=monogamy.

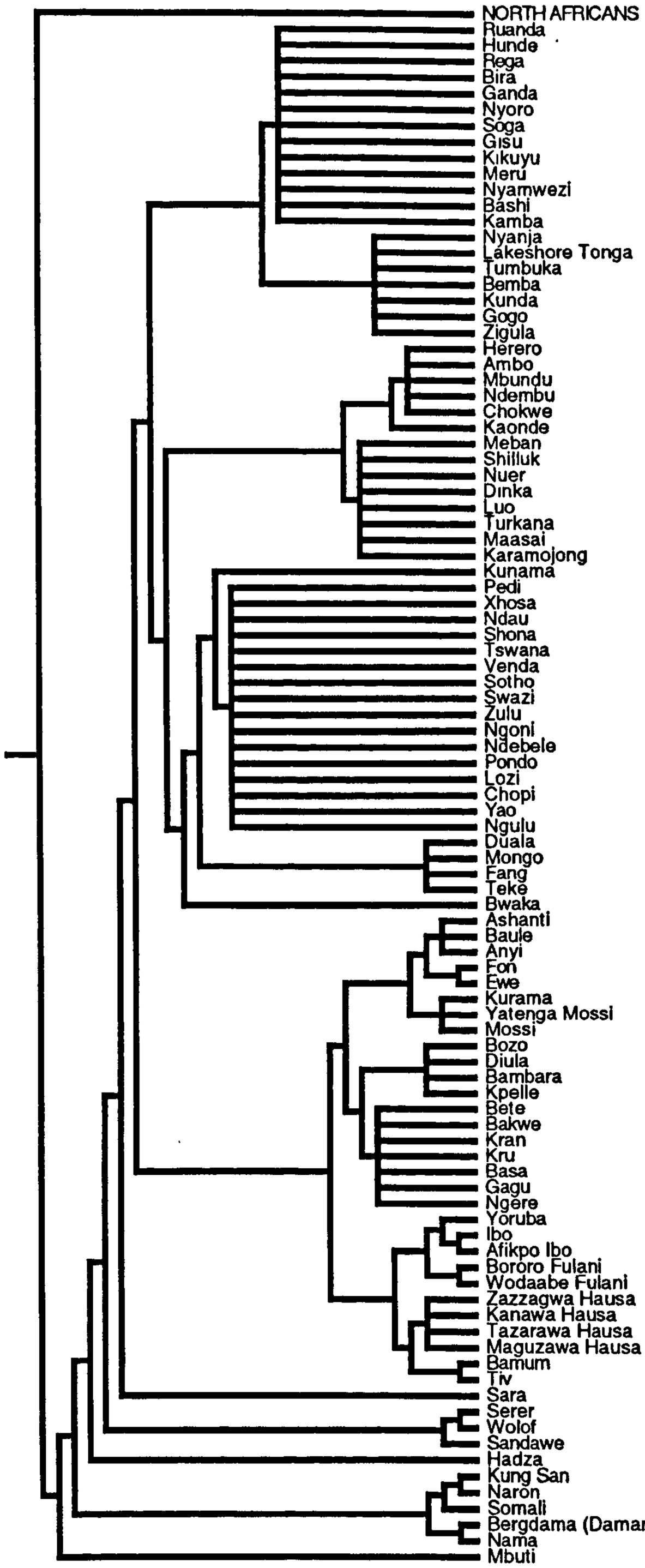


Figure 5.8A Genetic tree of Africa, adapted from Cavalli-Sforza et al. (1994), shown over two pages. On this page, sub-Saharan Africans are shown. Sub-Saharan Africans and North Africans (next page) are co-ordinate on this tree.

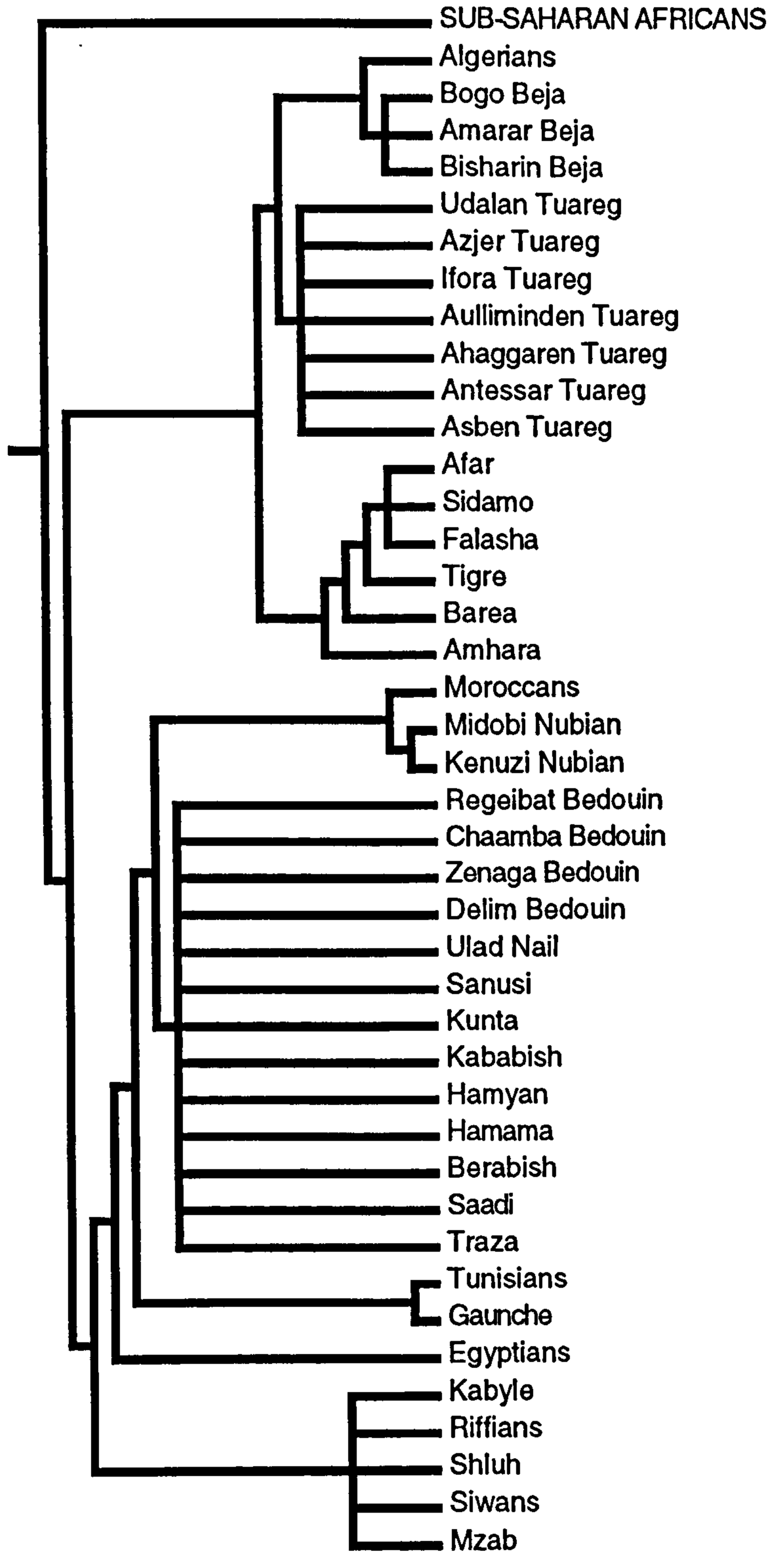


Figure 5.8B Genetic tree of Africa, adapted from Cavalli-Sforza et al. (1994), shown over two pages. On this page, North Africans are shown. North Africans and Sub-Saharan Africans (previous page) are co-ordinate on this tree.

5.3.2 The transmission of cultural traits

Aim. The aim of this part of the analysis was to investigate the transmission, between populations, of the cultural traits in the analysis. The aim was to test whether the cultural traits in the analysis were associated with population history, indicating vertical transmission from 'mother' to 'daughter' populations, and/or with geographical proximity to similar populations, indicating transmission by diffusion between neighbouring populations.

Geographical distribution of cultural traits. The geographical distribution of inheritance rules for movable property and land in Africa was shown in Figures 5.1 and 5.2 (section 5.1). The geographical distribution of dependence on livestock is shown in Figure 5.9. Livestock are rare in much of central Africa, especially in areas infested by the tsetse fly, where cattle cannot be kept (Aberle, 1961). Agro-pastoralist cultures (30-50% reliance on livestock) are found north, south and east of the tsetse belt. High levels of pastoralism are found in North Africa and in the Horn of Africa. The geographical distribution of marriage practices in Africa is shown in Figure 5.10. Monogamy is confined to North Africa. Sub-Saharan Africa has higher levels of polygyny than North Africa. 'General polygyny' is the most common type of marriage in sub-Saharan Africa.

Geographical clustering among traits may be compared to the clustering of the same traits mapped onto genetic and linguistic trees, used as models of the past relationships among populations (Figs 5.4 to 5.9). It is difficult to tell by eye whether

the clustering of character states on a map or tree is the result of geographical diffusion or vertical transmission, because closely related cultures tend to remain near the habitat of their ancestors. Statistical analysis was carried out to test whether vertical inheritance or horizontal diffusion, or both, are responsible for these effects.

Figure 5.9 Pastoralism in Africa

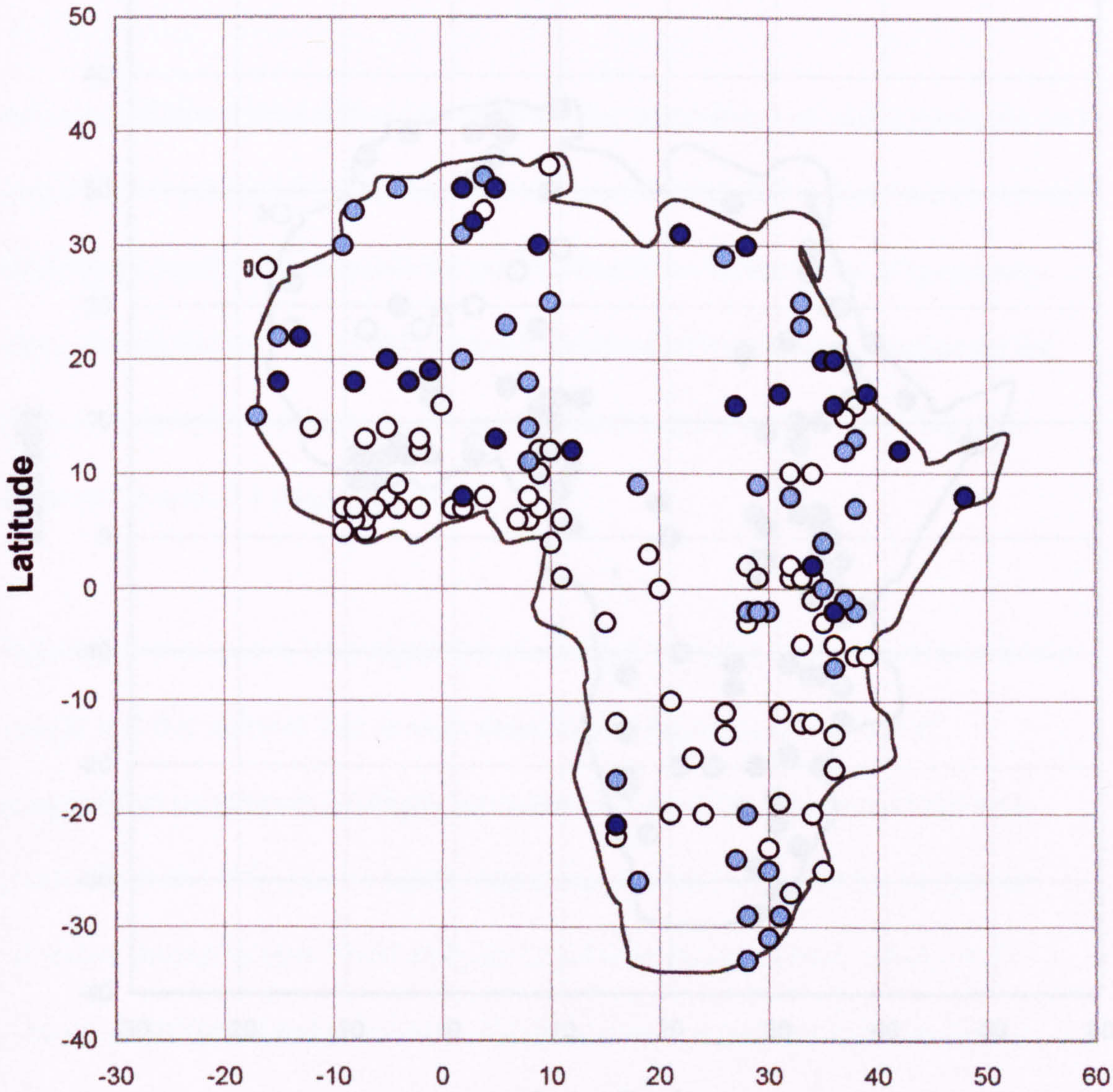
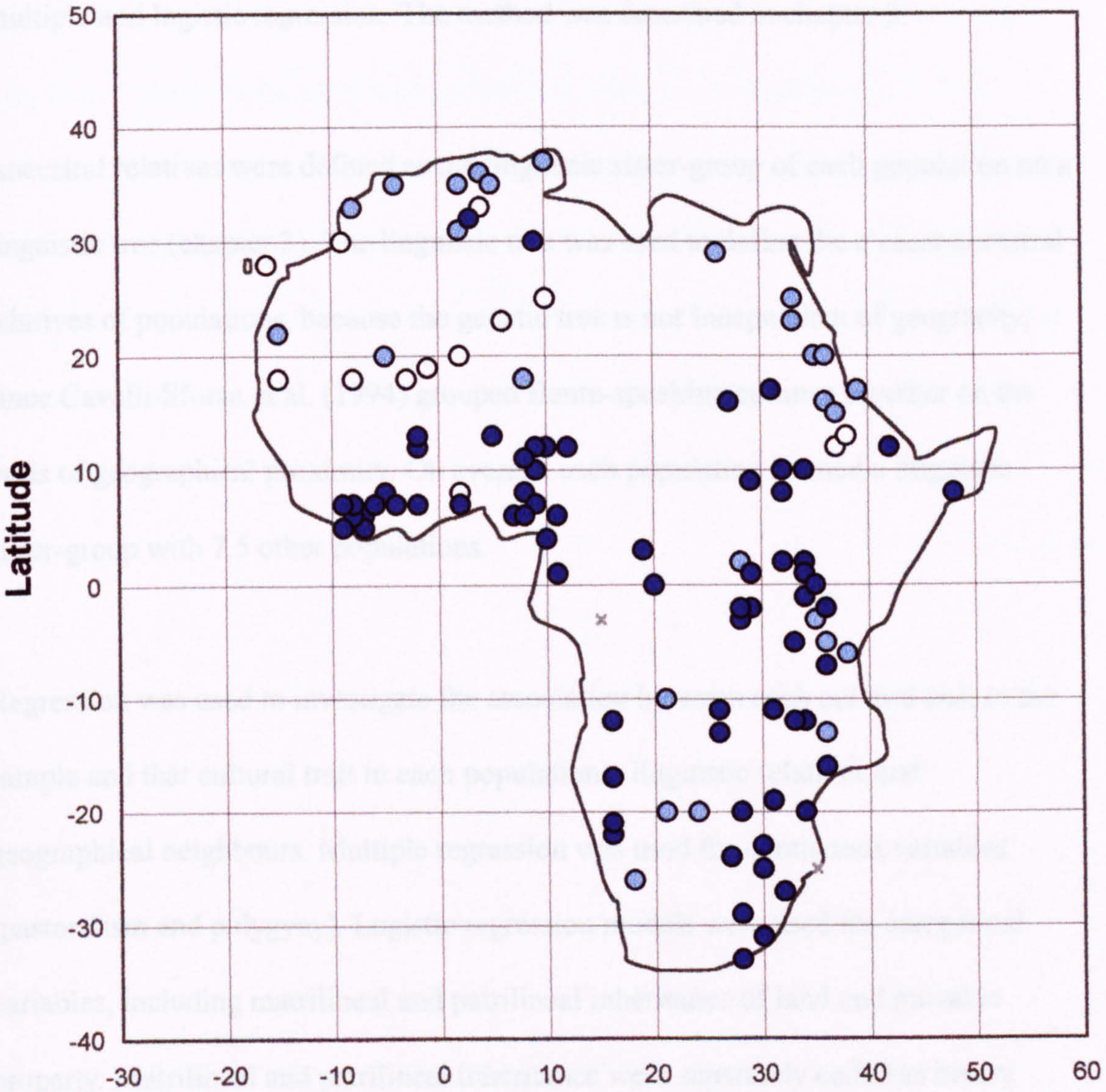


Figure 5.10 Polygyny in Africa



Statistical analysis. It was tested whether cultural traits were associated with populations' closest linguistic relatives and/or their geographical neighbours, using multiple and logistic regression. The method was described in chapter 3.

Ancestral relatives were defined as the linguistic sister-group of each population on a linguistic tree (chapter 3). The linguistic tree was used to define the closest ancestral relatives of populations, because the genetic tree is not independent of geography, since Cavalli-Sforza et al. (1994) grouped Bantu-speaking cultures together on the basis of geographical proximity. On average each population formed a linguistic sister-group with 7.5 other populations.

Regression was used to investigate the association between each cultural trait in the sample and that cultural trait in each population's linguistic relatives and geographical neighbours. Multiple regression was used for continuous variables (pastoralism and polygyny). Logistic regression models were used for categorical variables, including matrilineal and patrilineal inheritance of land and movable property. Matrilineal and patrilineal inheritance were separately coded as binary characters (for presence/absence of each type of inheritance). They were counted as present if they occurred in 50% or more of populations in a cluster. (The absence of matriliny does not necessarily imply the presence of patriliny, because other inheritance rules exist, see Table 5.2).

Results. All cultural traits tested showed a highly significant association with phylogeny. The level of polygyny showed an additional association with geographical neighbours. Pastoralism showed a marginally significant association with

geographical neighbours. The results are shown in Table 5.4 and 5.5. In the logistic regression (Table 5.4) the coefficient indicates the change in the log odds for the dependent variable when the independent variable is negative compared to positive (log odds = log[probability present/probability absent]). A negative coefficient indicates that the probability of the dependent variable being positive (present) is lower if the independent variable is negative (absent). In other words, a negative coefficient indicates that there is a positive correlation between the independent and dependent variables.

Table 5.4 The transmission between populations of cultural traits (categorical variables)

Logistic regression results, showing the association of categorical cultural traits with linguistic relatives and nearest neighbours. A negative coefficient indicates a positive relationship between the independent and dependent variables. Significance values shown are of partial coefficients. All logistic regression models were highly significant overall (chi-square log likelihood significant at 0.0002 or less).

	Linguistic relative(s)			**Geographical neighbour(s)**		
Dependent variable	**Estimated coefficient**	**S.E. of coefficient**	**Significance (Wald test)**	**Estimated coefficient**	**S.E. of coefficient**	**Significance (Wald test)**
			Matrilineal inheritance			
Land	-1.5129	.3514	<0.0001	-.1743	.4428	n.s.
Movable property	-1.4867	.3832	<0.0001	-.1746	.4055	n.s.
			Patrilineal inheritance			
Land	-.7337	.2321	0.002	-.2421	.2322	n.s.
Movable property	-1.0485	.2481	<0.0001	-.4114	.2465	n.s.

Table 5.5 The transmission between populations of cultural traits (continuous variables)

Multiple regression results showing the association between continuous variables and cultures' linguistic relatives and nearest geographical neighbours. The significance values shown are of partial regression coefficients. All multiple regressions were highly significant overall ($p<0.0002$).

	Linguistic relative(s)			Geographical neighbour(s)		
Dependent variable	**Slope**	**S.E. of slope**	**Significance of slope**	**Slope**	**S.E. of slope**	**Significance of slope**
Pastoralism	.6912	.0768	<0.0001	.6912	.0962	0.06
Polygyny	.7821	.0758	<0.0001	.1803	.0796	0.03

5.3.3 Comparative analysis of pastoralism, polygyny and inheritance

Aims. The aim in this part of the analysis was to test whether pastoralism is associated with patrilineal inheritance, and whether it is negatively associated with matrilineal inheritance. It also aimed to test whether polygyny is associated with patrilineal inheritance, and negatively associated with matrilineal inheritance.

Statistical analysis. Correlated change in inheritance, pastoralism and polygyny was investigated using comparative analysis using independent contrasts (Felsenstein 1985, Pagel 1992). The cross-cultural sample was the 138 culture African sample described in section 5.3.1. The genetic and linguistic trees described in section 5.3.1 were also used.

To perform a comparative analysis using independent contrasts (using CAIC), multi-state categorical variables such as descent and inheritance rules are re-coded as dichotomous categorical variables. For each character state, a new variable is created; 'state 1 versus all other states', 'state 2 versus other states', etc (Purvis and Rambaut, 1995). For the comparative analysis two dichotomous discrete variables on inheritance were created, 'patrilineal versus all others' and 'matrilineal versus all others'. Independent contrasts in other types of inheritance (e.g. son-biased inheritance) were not investigated separately because the number of cases was too small.

At nodes in the trees where there was a change in inheritance practices, contrasts in pastoralism and polygyny were generated, using the Brunch procedure of the computer program CAIC (Purvis and Rambaut, 1995). A single sample Student's t-test was carried out on contrasts in the independent variables (pastoralism and polygyny) at nodes on the tree where the dependent variable (inheritance) changed. Under the null hypothesis that the adoption of patrilineal or matrilineal inheritance is not associated with livestock or polygyny, the average change in these variables at nodes on the tree where inheritance rules changes is expected to be zero.

The relationship between independent contrasts in the two independent variables (pastoralism and polygyny) was also tested using multiple regression. If the assumption that livestock are used to pay bridewealth is correct, then one would expect pastoralism and polygyny to be correlated.

Results. Independent changes in pastoralism are significantly associated with increases in polygyny as predicted. Although significant, the value of r^2 is low (r^2 = 0.08). Some variation in polygyny is associated with livestock, but other factors must also play a role.

Summary statistics of contrasts in pastoralism and polygyny at nodes on the trees where changes in inheritance occur are shown in Table 5.6 (linguistic tree) and Table 5.7 (genetic tree). In these tables, the first column lists the variables tested (pastoralism and polygyny). The second column shows the number of contrasts (i.e. the number of independent contrasts in inheritance rules) in each analysis. The third

and fourth columns show the mean and standard error of contrasts in pastoralism and polygyny. The fifth and sixth columns show 95% confidence intervals for contrasts in pastoralism and polygyny. The final two columns show the t-value of the distribution of contrasts, and the significance of the t-value (degrees of freedom = number of cases minus one). The t-values show whether or not these distributions differ significantly from zero.

On the language tree, changes to patrilineal inheritance of movable property were associated with an increase in dependence on livestock and also with an increase in polygyny. Changes patrilineal inheritance of land were significantly associated with increased polygyny but were not associated with a significant change in pastoralism. This is not surprising, as the adoption of patrilineal inheritance of land would be expected to occur when land became a valuable resource, not when livestock became more important in the local economy. Changes to matrilineal inheritance for land and movable property was associated with a decrease in pastoralism. Changes to matrilineal inheritance were not associated with a significant change in polygyny, although the decrease in polygyny at changes to matrilineal inheritance of movable property were marginally significant ($p<0.1$). All non-significant results were in the expected direction.

On the genetic tree, changes to patrilineal inheritance of movable property were associated with a significant increase in pastoralism. Changes to patrilineal inheritance of land were not associated with a significant change in pastoralism. There was no significant association between changes to patrilineal inheritance and polygyny. Changes to matrilineal inheritance of land and movable property were

associated with a significant decrease in pastoralism. Changes to matrilineal inheritance of land and movable property were not associated with a significant decrease in polygyny, although the decrease in polygyny associated with changes to matrilineal inheritance of land was marginally significant ($p<0.1$). All non-significant results were in the expected direction.

Table 5.6 Contrasts in polygyny and pastoralism on the linguistic tree

Variable	No. of contrasts	Mean	S.E. mean	Lower C.I.	Upper C.I.	t-value	2-tailed sig.
Independent changes to patrilineal inheritance of movable property							
Pastoralism	22	4.8429	2.025	0.632	9.054	2.39	0.026
Polygyny	21	0.1016	0.043	0.013	0.191	2.38	0.027
Independent changes to patrilineal inheritance of land							
Pastoralism	23	1.2779	1.970	-2.808	5.364	0.65	0.523
Polygyny	23	0.1030	0.039	0.023	0.183	2.66	0.014
Independent changes to matrilineal inheritance of movable property							
Pastoralism	12	-7.4900	2.235	-12.409	-2.571	-3.35	0.006
Polygyny	11	-0.1440	0.071	-0.302	0.014	-2.03	0.070
Independent changes to matrilineal inheritance of land							
Pastoralism	12	-5.4326	2.155	-10.175	-0.690	-2.52	0.028
Polygyny	11	-0.1615	0.092	-0.365	0.042	-1.76	0.108

Table 5.7 Contrasts in polygyny and pastoralism on the genetic tree

Variable	No. of contrasts	Mean	S.E. mean	Lower C.I.	Upper C.I.	t-value	2-tailed sig.
Independent changes to patrilineal inheritance of movable property							
Pastoralism	20	4.6004	1.912	0.599	8.602	2.41	0.026
Polygyny	19	0.0506	0.046	-0.046	0.147	1.10	0.285
Independent changes to patrilineal inheritance of land							
Pastoralism	20	0.2881	2.071	-4.046	4.623	0.14	0.891
Polygyny	20	0.0217	0.031	-0.043	0.086	0.07	0.491
Independent changes to matrilineal inheritance of movable property							
Pastoralism	11	-7.9917	2.314	-13.147	-2.836	-3.34	0.006
Polygyny	10	-0.1342	0.079	-0.314	0.045	-1.69	0.125
Independent changes to matrilineal inheritance of land							
Pastoralism	11	-7.7602	2.049	-12.326	-3.195	-3.79	0.004
Polygyny	10	-.1555	0.0.84	-0.345	0.034	-1.86	0.097

5.3.4 Inferring causality in the co-evolution of pastoralism and inheritance

Aim. The hypothesis tested here was that patrilineal descent is correlated with cattle keeping. Pagel's (1994) maximum likelihood model was used to investigate the direction of evolutionary change in these two characters.

Data. A different sample was used, because Pagel's (1994) method analyses discrete binary categorical variables, and requires all cultures to be placed on a fully resolved phylogeny. The sample included those 79 sub-Saharan African cultures in the *Ethnographic Atlas* (Murdock, n.d.) that had clearly unilineal descent, and which could be placed on Cavalli-Sforza et al.'s (1994) African genetic tree. The two variables hypothesised to be correlated were patrilineal descent and cattle keeping. Descent is a composite measure of inheritance of land and movable property and rules of succession. Cultures with double descent (meaning that an individual is a member of his father's patrilineal group and his mother's matrilineal group) were counted as patrilineal, because these cultures had patrilineal wealth inheritance. Data on the presence of cattle were taken from the *Ethnographic Atlas* (Murdock, n.d.).

Statistical analysis. Pagel's (1994) maximum likelihood method for testing for correlated evolution in discrete characters was used to test for correlated evolution in patriliny and pastoralism. The significance of each transition in the model was also

investigated. The method was described in chapter 3. The tree used was based on Cavalli-Sforza et al.'s (1994) F_{ST} genetic tree of African populations. Unresolved nodes were resolved on linguistic similarity where possible. Where nodes could not be resolved, and the cultures showed no variation in the relevant characters, they were clumped into a single tip. Pagel's maximum likelihood model was also used to investigate the direction of evolutionary change in cattle keeping and pastoralism.

Results. The 79 cultures in this sample are shown in Figures 5.11 and 5.12. In Figure 5.11, descent rules are shown mapped onto the tree using parsimony (using the computer program MacClade, Maddison and Maddison, 1992). In Figure 5.12, the presence of cattle is shown mapped onto the tree. The most parsimonious reconstruction of ancestral character states is not the only reconstruction considered when fitting a maximum likelihood model to the data; parsimony was used in the figures for illustrative purposes only.

The likelihood of the dependent model was significantly higher than the likelihood of the independent model (p=0.02). This indicates that transitions to patriliny and cattle keeping are correlated. The rate and significance of each character transition is shown in Figure 5.13. A high rate of change for a particular character transition does not necessarily indicate that this transition is significant in the model. Significant character transitions, calculated by setting the rate of that transition to zero and testing the likelihood of the restricted model against the unrestricted model, are indicated by black arrows. The results suggest that transitions between matriliny and patriliny are possible for cultures which lack cattle. Once a population gains cattle it appears unlikely that they will lose them. The transition from matriliny without cattle

to patriliny with cattle is most likely to occur via the state of matriliny with cattle, suggesting that patriliny follows from becoming pastoralist. The state of patriliny with cattle appears to be stable: transitions away from this state are not significant in the model.

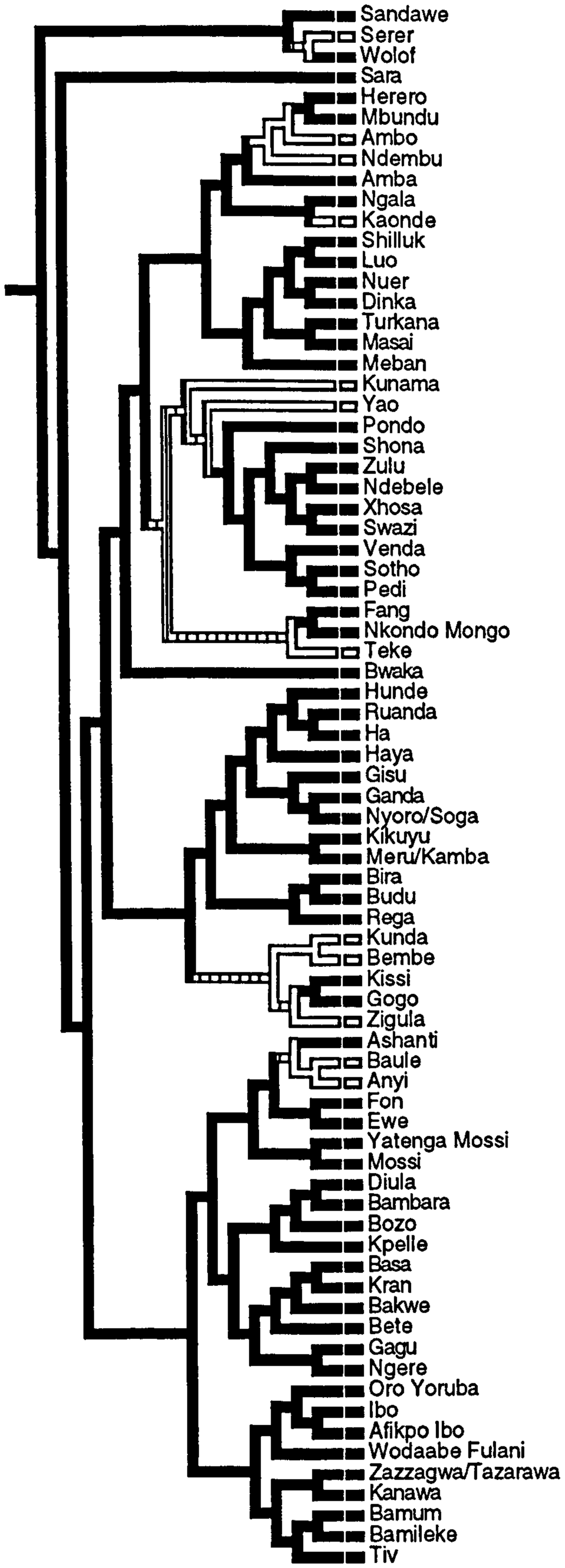


Figure 5.11 Composite tree of 79 cultures in sub-Saharan Africa, based on Cavalli-Sforza et al.'s (1994) F_{ST} genetic tree. Descent is mapped onto the tree using parsimony, using MacClade (Maddison and Maddison, 1994). The most parsimonious reconstruction of ancestral states (shown here) is only one of the possible reconstructions considered in the maximum likelihood model. Black indicates patriliny, grey indicates duolateral descent, and white indicates matrilineal descent. Hatched lines indicate ambiguous ancestral states.

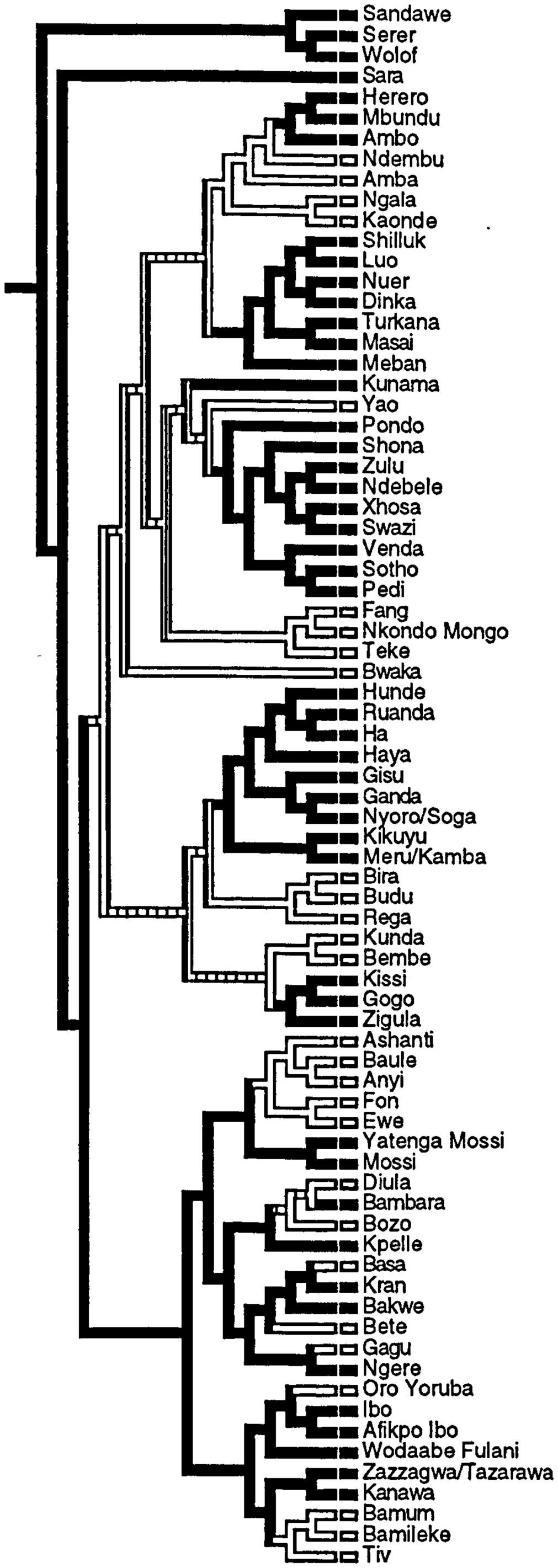
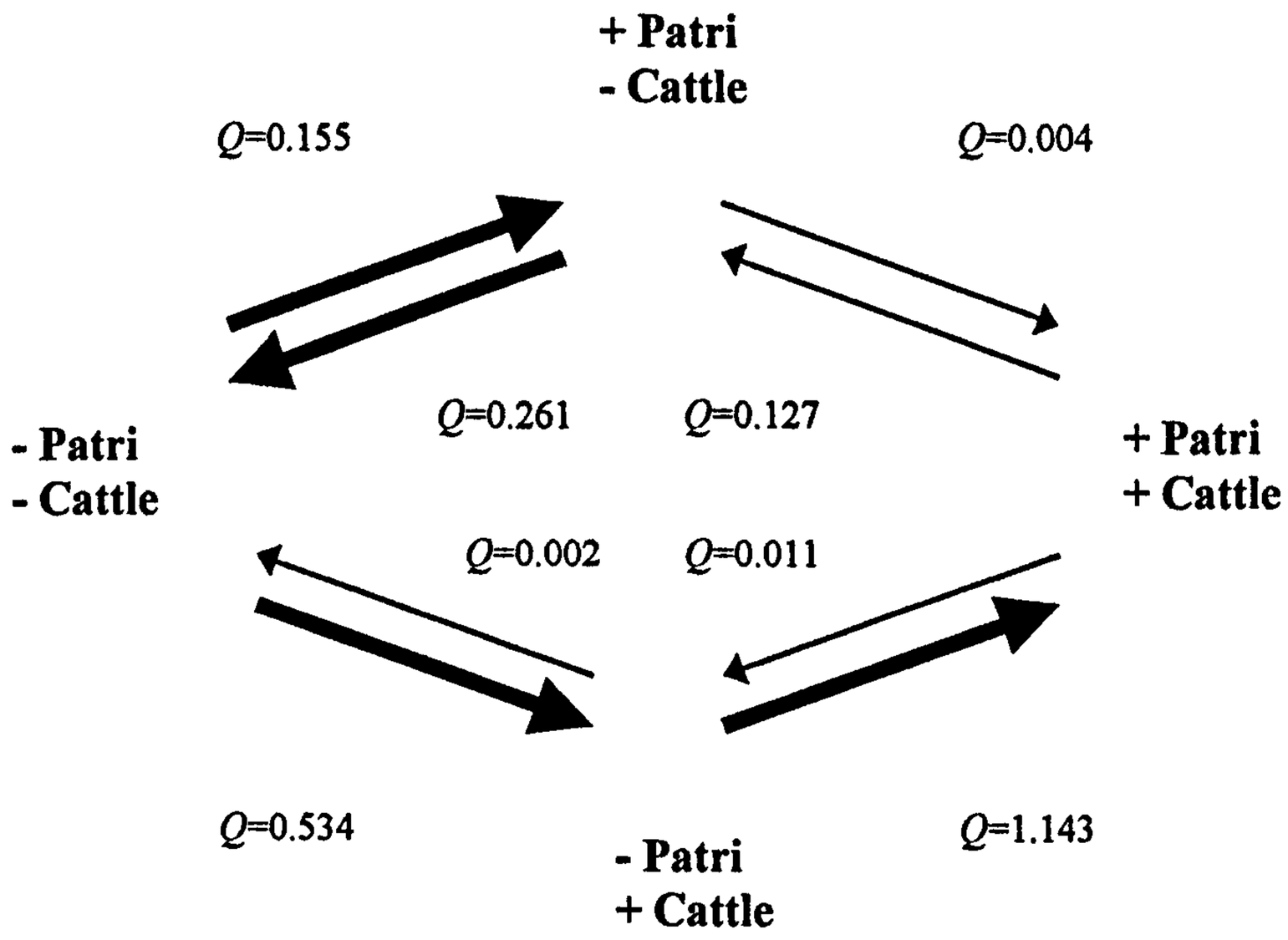


Figure 5.12 Composite tree of 79 cultures in sub-Saharan Africa, based on Cavalli-Sforza et al.'s (1994) F_{ST} genetic tree. Cattle keeping is mapped onto the tree using parsimony, using MacClade (Maddison and Maddison, 1994). Black indicates presence of cattle, white indicates absence of cattle. Hatched lines indicate ambiguous ancestral states.

Figure 5.13 A likelihood model of transitions in pastoralism and descent

The rate and significance of transitions between character states are shown. *Q* values indicate the rate of transition between two states in the model. Black arrows indicate transitions that are significant at the $p < 0.01$ level.



5.3.5 Comparative analysis of paternity uncertainty and inheritance

Aim. The aim of this part of the analysis was to re-test Flinn's (1981) finding that the direction of altruism to kin is associated with the level of paternity uncertainty, using a method that controls for Galton's problem.

Data. Data on paternity uncertainty from Flinn (1981) were used. This is the largest, and probably best quality, source of cross-cultural data on paternity uncertainty. Flinn's (1981) dataset includes 300 cultures worldwide. There were 69 African cultures in Flinn's sample, of which 60 were used here (Table 5.8). Of the 9 cultures not used here, 7 were excluded because their language was unknown (not in Ruhlen, 1991) and 2 were from Madagascar which is not counted as Africa by Murdock (1967). In addition, the Chagga had no data on paternity confidence and male altruism. Of the 60 cultures in the sample, 30 are also found in the 138 culture African sample. Flinn identified cultures using codes from the Outline of World Cultures (OWC). O'Leary (1969) provides a concordance between OWC codes and *Ethnographic Atlas* codes.

Flinn (1981) coded paternity confidence on an ordinal scale from 1 to 5 (low to high) using data from the Human Area Relations Files. Actual levels of paternity probability were not specified. He reported a high level of replicability when Laura Betzig re-coded part of his sample. Flinn also used a scale from 1 to 5 to code variation in the

direction of altruism to kin, from exclusively agnatic to exclusively uterine kin. He used data on the flow of material benefits among kin (from the Human Area Relations Files) not professed sentiments. His scores on the direction of flow of altruism for kin are closely correlated with Murdock's (1967) data on wealth inheritance (Table 5.8).

Table 5.8 Paternity confidence and altruism to kin in 60 African cultures

Cultures' names and *Ethnographic Atlas* (EA) codes are shown. Flinn's (1981) data on paternity confidence (1= lowest, 5=highest) and the direction of altruism (1=most uterine, 5=most agnatic) are shown. Murdock's (1967) data on inheritance rules for land and movable property are shown (cols. 5 and 6) so they can be compared to Flinn's codes on the direction of altruism to kin.

Name	EA code	Paternity confidence	Altruism to kin	Inheritance of land	Inheritance of movables
Amhara	Ca7	4	1	No rules	Patrilineal
Ashanti	Af3	3	4	Matrilineal	Matrilineal
Azande	Ai3	4	1	Patrilineal	Patrilineal
Bassa	Ah11	4	1	Patrilineal	Patrilineal
Beja	Ca5	5	1	Missing data	Patrilineal
Bemba	Ac3	3	4	Matrilineal	Matrilineal
Beraber	Cd7	5	1	Patrilineal	Patrilineal
Bijogo	Ag18	3	4	Matrilineal	Matrilineal
Birifor	Ag5	3	2	Patrilineal	Matrilineal
Chagga	Ad3	Missing data	Missing data	Patrilineal	Patrilineal
Chamba	Ah28	3	2	Patrilineal	Matrilineal
Chokwe	Ac12	3	4	Matrilineal	Matrilineal
Dagom[14] (Dogon)	Ag3	3	2	Patrilineal	Patrilineal
Dera	Cb28	3	2	Missing data	Missing data
Egyptians	Cd2	5	1	Son biased	Son biased
Fur	Cb17	4	3	Patrilineal	Patrilineal
Ga	Af43	3	2	Patrilineal	Patrilineal

[14] Dagom is an ethnonym of Dogon.

Table 5.8 (cont.)

Name	EA code	Paternity confidence	Altruism to kin	Inheritance of land	Inheritance of movables
Ganda	Ad7	4	1	Patrilineal	Patrilineal
Guanche	Cd11	4	3	Matrilineal	Matrilineal
Gure	Ah6	3	4	Matrilineal	Matrilineal
Hausa (Zazzagwa)	Cb26	4	2	Son biased	Son biased
Hehe	Ad8	4	2	Missing data	Son biased
Herero	Ab1	3	2	No rules	Matrilineal
Ila	Ac1	3	3	No rules	Matrilineal
Ingassana	Ai4	4	1	Missing data	Missing data
Jukun	Ah2	4	2	Patrilineal	Patrilineal
Kadara	Ah19	4	2	Patrilineal	Patrilineal
Kikuyu	Ad4	5	1	Patrilineal	Patrilineal
Kissi	Af2	4	1	Patrilineal	Patrilineal
Kongo	Ac14	3	4	Matrilineal	Matrilineal
Kpe	Ae2	4	2	Patrilineal	Missing data
Kuba	Ac4	3	4	No rules	Matrilineal
Kunama	Ca33	4	3	Matrilineal	Matrilineal
Lamba	Ac5	3	4	Missing data	Matrilineal
Lobi	Ag11	4	3	To children	Matrilineal
Lovedu	Ab14	4	2	Missing data	Patrilineal
Lozi	Ab3	4	2	Patrilineal	Patrilineal
Luimbe	Ac28	3	3	Matrilineal	Matrilineal
Margi	Ah5	4	2	Patrilineal	Patrilineal
Masai	Aj2	5	2	Patrilineal	Patrilineal
Mbugwe	Ad5	4	2	Patrilineal	Patrilineal
Mbundu	Ab5	4	2	Patrilineal	Matrilineal
Mende	Af5	4	2	Patrilineal	Patrilineal
Merina	Eh2	5	1	To children	To children

Table 5.8 (cont.)

Name	EA code	Paternity confidence	Altruism to kin	Inheritance of land	Inheritance of movables
Mesakin	Ai39	3	4	Mixed matrilineal and patrilineal	Mixed matrilineal and patrilineal
Mossi	Ag47	4	1	Patrilineal	Patrilineal
Nama	Aa3	4	2	No rules	Patrilineal
Ndoro	Ah26	2	5	Matrilineal	Matrilineal
Ngoni	Ac9	4	2	Patrilineal	Patrilineal
Nuer	Aj3	5	1	Patrilineal	Patrilineal
Nyakyusa	Ad6	4	2	Patrilineal	Patrilineal
Nyaneka	Ab7	3	4	Matrilineal	Matrilineal
Sandawe	Aa6	5	2	Missing data	Patrilineal
Serer	Ag22	4	4	Matrilineal	Patrilineal
Shawiya	Cd8	5	1	Patrilineal	Patrilineal
Somali	Ca2	5	1	Son biased	Son biased
Tallensi	Ag4	4	2	Patrilineal	Patrilineal
Tanala	Eh3	3	2	Patrilineal	To children
Tenda	Ag8	3	3	Matrilineal	Matrilineal
Thonga	Ab4	4	2	No rules	Patrilineal
Tiv	Ah3	4	2	No rules	Patrilineal
Tswana	Ab13	5	2	Patrilineal	Patrilineal
Tuareg (Ahaggaren)	Cc9	3	3	Matrilineal	Son biased
Tullishi	Ai42	4	2	Mixed matrilineal and patrilineal	Patrilineal
Ulad Nail	Cd17	5	1	Patrilineal	Son biased
Wolof	Cb2	4	2	Son biased	Son biased
Yako	Af4	4	3	Patrilineal	Matrilineal
Yao	Ac7	3	4	Missing data	Matrilineal
Yoruba (Oyo)	Af6	4	1	Patrilineal	Patrilineal

Statistical analysis. Comparative analysis using independent contrasts was used to test the relationship between paternity uncertainty and the direction of altruism (Felsenstein, 1985; Pagel, 1992; Pagel, 1993). The past relationships among the 60 populations in the sample were estimated using a linguistic tree, adapted from Ruhlen (1991), assuming equidistance among language phyla, and a single origin of language phyla. A linguistic tree was used rather than a genetic tree because the linguistic tree is much better resolved for sub-Saharan African cultures. Independent contrasts in paternity confidence and the direction of altruism were generated using the computer program CAIC (Purvis and Rambaut, 1995). Paternity confidence was used to resolve unresolved nodes on the tree, after the method of Pagel (1992). The tree generated 38 independent contrasts. Regression through the origin was used to investigate the relationship between changes in the independent variable (paternity confidence) and the dependent variable (the direction of altruism to kin), using SPSS (Norušis, 1994).

Results. Flinn's (1981) data on paternity confidence are shown, mapped onto the linguistic tree using parsimony, in Figure 5.14. His data on the direction of altruism to kin are shown mapped onto the linguistic tree in Figure 5.15. There was a highly significant relationship between independent contrasts in paternity confidence and the direction of altruism to kin, shown in Table 5.9. Altruism is directed more towards uterine kin when paternity confidence is decreased and more towards agnatic kin when paternity confidence is increased. This is consistent with evolutionary predictions (section 5.2.2), and is evidence that the cross-cultural correlation between low paternity confidence and matriliny, observed by Gaulin and Schlegel (1980), Flinn (1981), Hartung (1981), and Hartung (1985) is not an artefact of non-independence among populations.

Table 5.9 Regression of contrasts in altruism to kin on paternity confidence

Overall regression model		**Relationship between increased uterine bias in altruism and paternity confidence**	
Multiple R	.73	**Slope**	-1.3262
Adjusted R^2	.53	**S.E. slope**	.202
F	43.25	**Significance of slope**	<0.0001
Significance F	<0.0001		

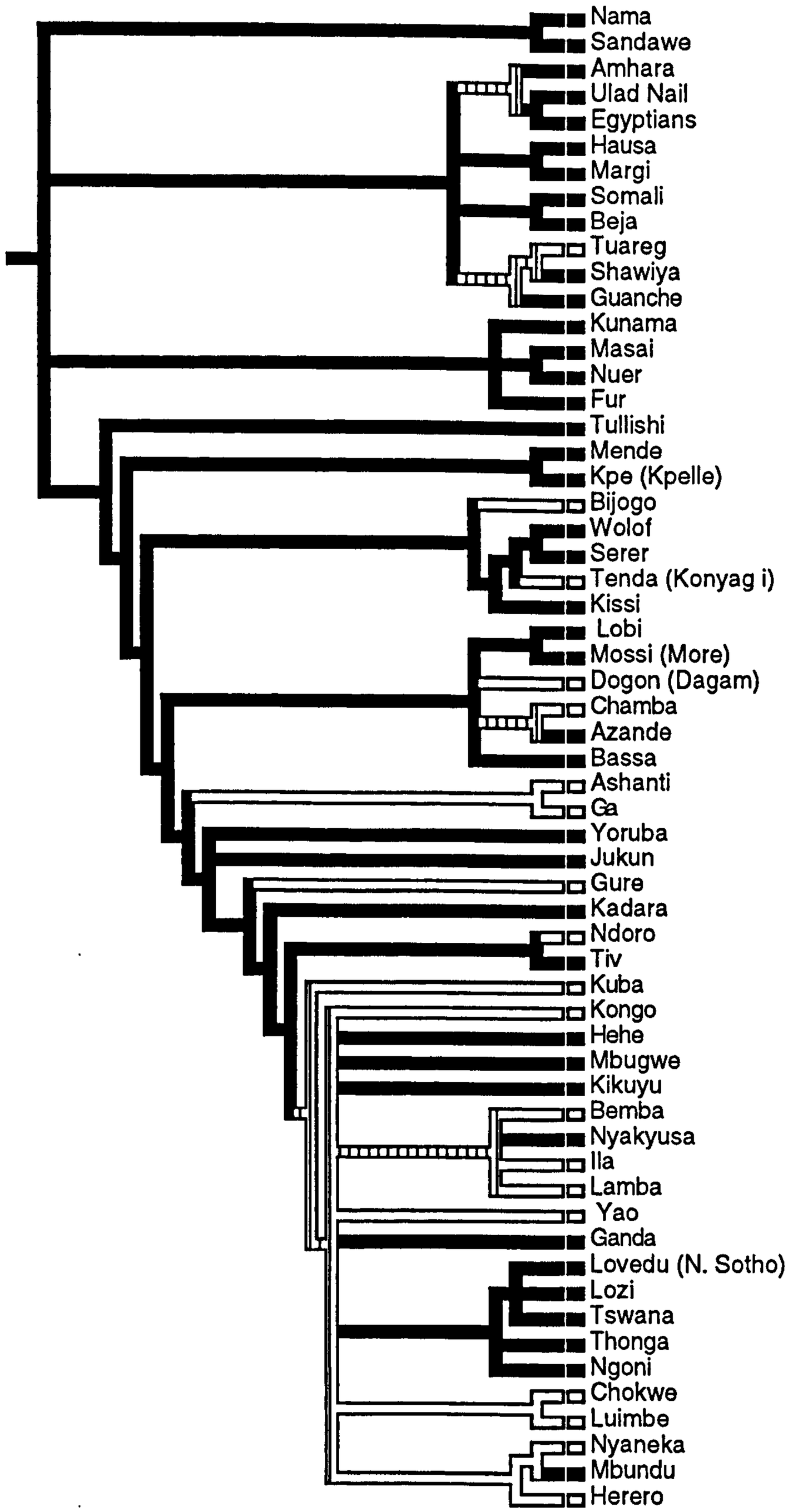


Figure 5.14 Linguistic tree of 60 African cultures (adapted from Ruhlen, 1991), showing paternity confidence, grouped into two categories for illustrative purposes. Black= high paternity confidence (Flinn's codes 4 and 5), white=medium to low paternity confidence (Flinn's codes 2 and 3).

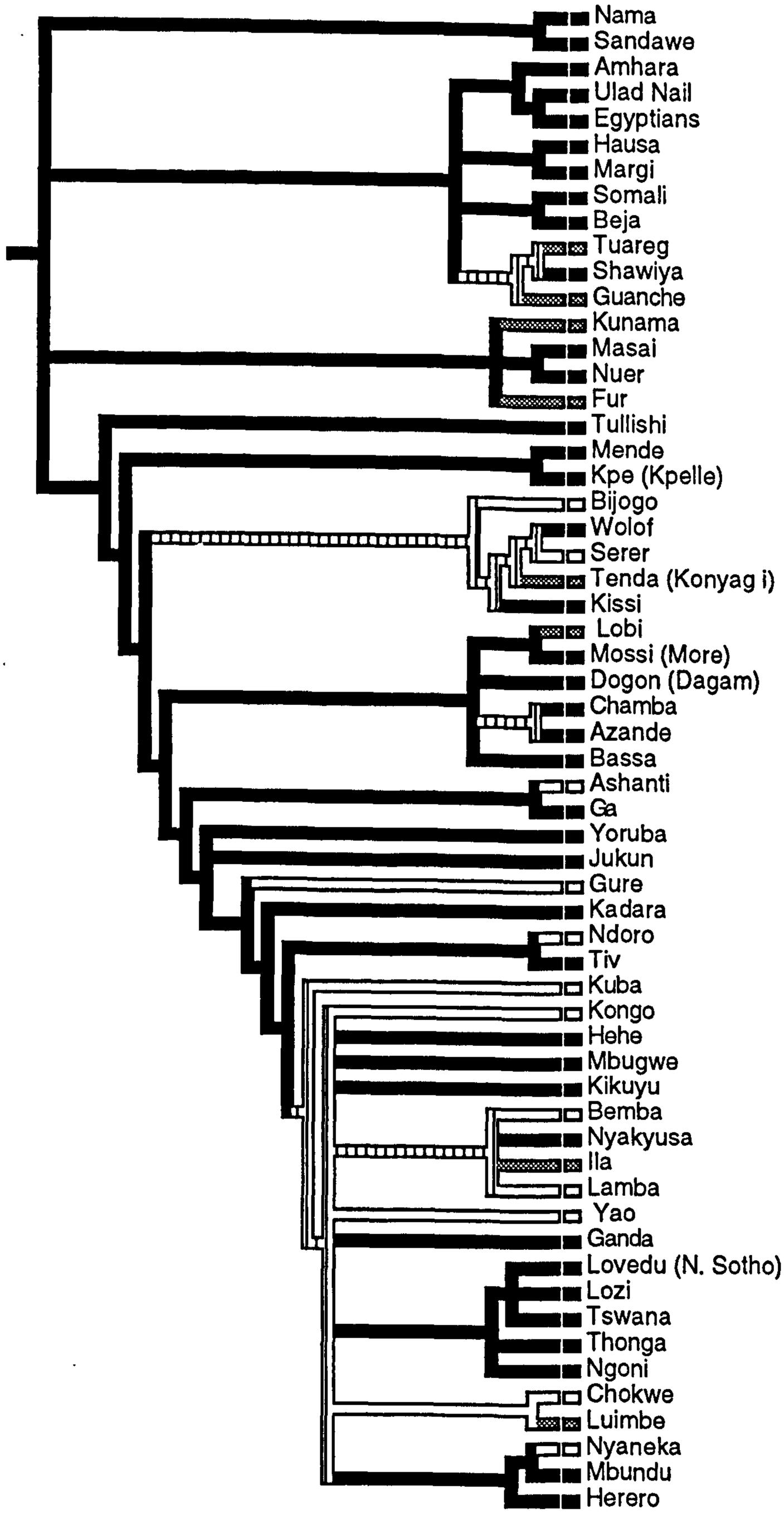


Figure 5.15 Linguistic tree of 60 African cultures (adapted from Ruhlen, 1991), showing direction of altruism to kin, grouped into three categories for illustrative purposes. Black= agnatic bias (Flinn's codes 4 and 5), grey=no bias (Flinn's code 3), white=uterine bias (Flinn's codes 1 and 2).

5.4 Conclusions and discussion

All cultural traits (inheritance practices and amount of pastoralism and polygyny) showed a highly significant association with linguistic descent groups. This indicates that these traits are transmitted vertically, from 'mother' to 'daughter' cultures. Polygyny and pastoralism showed an additional association with nearest geographical neighbours. This indicates that they are also transmitted horizontally and/or are adaptations to the environment. Diffusion of all traits between neighbouring populations appears to be less significant than vertical transmission. Genetic trees are probably better models of population history than linguistic trees, and it would be interesting to test whether the cultural traits in the analysis showed an association with a genetic phylogeny. However, as mentioned above, the genetic tree used here was not independent of geography so this test could not be done (Cavalli-Sforza et al., 1994).

Patriliny was found to be associated with pastoralism, polygyny and high paternity confidence. Matriliny was found to be negatively associated with pastoralism and polygyny, and associated with low paternity confidence. These results are consistent with the sociobiological prediction that parents should transmit wealth to sons if the benefits of inherited wealth are greater for sons than daughters (Trivers and Willard, 1973; Maynard Smith, 1980), which is expected to be the case if the wealth is sufficient to allow sons to marry polygynously (Orians, 1969; Mace, 1996). Otherwise, it is adaptive to transmit wealth to daughters, so it passes to grandchildren

whose relationship to the grandparent is confidently known (c.f. Euler and Weitzel, 1996). From the point of view of the grandmother, matrilineal inheritance of property through the mother's brother to the sister's son is functionally equivalent to inheritance from mother to daughter, in that her daughter's children inherit the wealth (Mace and Holden, 1999). As noted above (section 5.2.2), direct inheritance from mother to daughter may be more common than is often assumed.

In the cultural co-evolution of pastoralism and inheritance, pastoralism probably changes before inheritance. In Africa, patrilineal, pastoralist societies probably developed from matrilineal, pastoralist societies, rather than from patrilineal, non-pastoralist societies. Patriliny with pastoralism appears to be a stable condition. Once gained, cattle and patriliny are unlikely to be lost.

It would be interesting to test the direction of evolutionary change in paternity confidence and inheritance. Since this analysis was done, a new method has been developed, by Pagel (1998), which uses maximum likelihood to test for correlated evolution in continuous variables. It might be possible to apply this test to Flinn's ordinal variables on paternity confidence and the direction of altruism to kin. Like Pagel's (1994) method for testing for correlated evolution in discrete characters, this method can also be used to investigate the direction of evolutionary change in correlated variables. One wonders whether further support would be found for Morgan's (1877) model of cultural evolution, which seems to contain more than a grain of truth, despite being considered not worthy of consideration by many anthropologists (e.g. Schneider and Gough, 1961).

Chapter 6

Sexual dimorphism in stature and women's work[15]

6.0 Summary

Correlates of variance in sexual dimorphism in stature across 76 populations were investigated. Polygyny, the sexual division of labour, and hunting and agriculture were tested. The transmission of these traits among populations was also investigated. All traits were found to be associated with phylogeny. Felsenstein's (1985) method of comparative analysis using independent contrasts was used to control for the statistical effects of similarity due to common ancestry. Cross-cultural variance in sexual dimorphism in stature was found to be negatively associated with women's contribution to subsistence. Women are taller, relative to men, in societies where

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[15] A version of this chapter is published as: Holden C, Mace R. 1999. Sexual dimorphism in stature and women's work: a phylogenetic cross-cultural analysis. *American Journal of Physical Anthropology* 110:27-45.

women contribute more to food production. No relationship was found between sexual dimorphism and other aspects of subsistence or polygyny.

6.1 Sexual size dimorphism in humans

In all populations, mean male stature is greater than mean female stature, but there is variation in the level of sexual dimorphism among populations. In this chapter I will test for correlates of cross-cultural variance in sexual dimorphism in a worldwide sample of 76 populations. The aim was to test two hypotheses for cross-cultural variance in sexual dimorphism in stature, while controlling statistically for the non-independence of populations (Galton's problem).

The first hypothesis is that sexual dimorphism in stature is associated with polygyny, because intra-male competition for females (selecting for larger males) is higher in polygynous populations (Trivers, 1972; Alexander et al., 1979). The second hypothesis is that sexual dimorphism is associated with the sexual division of labour, because there are different selection pressures on male and female stature in populations where there is a marked sexual division of labour (Frayer, 1980; Brace and Ryan, 1980). Both theories descend from Darwin (1874), who suggested that sexual dimorphism can evolve both through sexual selection, and through natural selection in species where the two sexes occupy different ecological niches. These

hypotheses were first proposed to explain variance in sexual dimorphism across species, but may also explain part of the cross-cultural variation in sexual dimorphism in stature in humans.

It was tested whether the five bio-cultural traits in the analysis are associated with phylogeny, indicating vertical transmission, and/or geographical proximity among populations, indicating horizontal transmission. All traits were associated with phylogeny. Three out of five traits were also associated with geographical proximity. Felsenstein's (1985) method of comparative analysis using independent contrasts was used to control for the statistical effects of similarity due to common ancestry. Sexual dimorphism in stature is negatively correlated with women's overall contribution to subsistence. No relationship was found between sexual dimorphism and type of subsistence (hunting or agriculture) or polygyny.

6.2 Hypotheses for cross-cultural variation in sexual dimorphism

6.2.1 Polygyny

Darwin (1874) hypothesised that many aspects of sexual dimorphism, including size dimorphism, are sexually selected through competition among males for females in polygynous species. Across many mammalian groups, including pinnipeds, ungulates and non-human primates, size dimorphism is associated with polygyny (Alexander et al., 1979; Leutenegger, 1982; Andersson, 1994). Trivers (1972) hypothesised that cross-cultural variation in sexual dimorphism in humans may be associated with cross-cultural variation in mating or marriage patterns. A number of studies have tested this hypothesis.

Alexander et al. (1979) tested the hypothesis that sexual dimorphism in stature is greater in polygynous societies than in monogamous societies on a cross-cultural sample of 93 human populations. In their initial analysis, they found no difference in sexual dimorphism in stature between the 47 monogamous and 46 polygynous societies in the sample. They then divided the monogamous societies into two groups: 'ecologically' and 'socially' imposed monogamy. Ecologically imposed monogamy is

found in marginal habitats, for example among some hunter-gatherers. Alexander et al. (1979) argued that the ecological basis of this type of monogamy was the same as monogamous mating in other species, i.e. a relatively equal distribution of resources among males (Orians, 1969). In contrast, socially imposed monogamy occurs in societies where there is high variance in wealth and resources among males, i.e. where one would expect wealthy males to mate polygynously. Alexander et al. (1979) argued that socially imposed monogamy is a historically recent phenomenon, in which monogamy is imposed by the state. There were 16 societies in the sample with ecologically imposed monogamy, and 31 societies with socially imposed monogamy. The ratio of male to female stature in ecologically imposed monogamous societies was 1.068, as compared with 1.078 in polygynous and socially imposed monogamous societies (this difference was significant at the p=0.03 level).

Gray and Wolfe (1980) criticised Alexander et al.'s (1979) study for questionable use of data sources on stature, and for not using an independent source of information about marriage practices. In subsequent studies Murdock's (1967; 1986) *Ethnographic Atlas* has been used as a source of data about marriage across cultures. Gray and Wolfe (1980) found no difference in sexual dimorphism in stature between monogamous and polygynous populations using a sample of 140 populations, using data on marriage from Murdock's (1967) *Ethnographic Atlas*.

In a sample of 155 populations, Wolfe and Gray (1982a) found no difference in sexual dimorphism in stature between monogamous, 'occasionally polygynous' and 'generally polygynous' populations, using data on marriage from Murdock's (1967) *Ethnographic Atlas*. 'Occasional polygyny' means that fewer than 20% of marriages

are polygynous and 'general polygyny' means more than 20% of marriages are polygynous. Wolfe and Gray (1982a) also used information about social organisation from the *Ethnographic Atlas* to distinguish between ecologically imposed monogamy and socially imposed monogamy, replicating Alexander et al.'s (1979) original classification using an independent source of data on marriage. Ecologically imposed monogamy was defined as monogamy in non-state societies, and socially imposed monogamy was defined as monogamy in state societies. They found no difference in sexual dimorphism in stature between populations with ecologically imposed monogamy and other populations. Wolfe and Gray (1982a) also repeated their analysis using Alexander et al.'s (1979) original codes on ecologically and socially imposed monogamy. Using these codes they found that societies with ecologically imposed monogamy had lower sexual dimorphism in stature than other groups. However they concluded that this result may have been an artefact of unconscious bias by the original coders, since it was not replicated using the independent codes of Murdock's (1967) *Ethnographic Atlas.*

Gaulin and Boster (1992) used the same sample of 155 populations as Wolfe and Gray (1982a), and data on social stratification from Murdock (1986) to distinguish between ecologically and socially imposed monogamy, classifying monogamy in non-stratified societies as ecologically imposed, and monogamy in stratified societies as socially imposed. They found that populations with ecologically imposed monogamy were significantly less sexually dimorphic in stature than populations with socially imposed monogamy, thereby replicating Alexander et al.'s original (1979) results. However, this relationship disappeared when they excluded estimates of sexual dimorphism from samples of fewer than 10 individuals of each sex, suggesting

that it may have been an artefact of poorly sampled populations.

In summary, most previous studies do not support the hypothesis that cross-cultural variation in dimorphism in stature is associated with polygyny

6.2.2 The sexual division of labour

The second hypothesis also stems from Darwin (1874), who suggested that sexual dimorphism can evolve through natural selection in species where males and females occupy different ecological niches, for example if males and females have different foraging strategies. A mathematical model of the evolution of sexual dimorphism through ecological divergence between the sexes was formulated by Slatkin (1984). Evidence for the ecological niche hypothesis of sexual dimorphism in animals is reviewed by Shine (1989).

Human societies are characterised by marked sexual division of labour in subsistence activities, the human equivalent of animal foraging strategies (Murdock and Provost, 1973). Natural selection on traits related to food production may therefore be different in males and females. This hypothesis has been developed in palaeo-anthropology. Frayer (1980; 1981) and Brace and Ryan (1980) hypothesised that changes in the subsistence activities of males and females may explain the decline in sexual dimorphism since the Late Palaeolithic. Large-game hunting was a more

important subsistence activity in the Late Palaeolithic than in later periods (Frayer, 1981). In contemporary populations, large-game hunting is almost exclusively a male activity (Murdock and Provost, 1973). By ethnographic analogy, it was probably also a male activity in the Late Palaeolithic. It is hypothesised that males in the Late Palaeolithic were selected for physical strength and size because they hunted large animals using spears (Frayer, 1980; 1981, Brace and Ryan, 1980). Selection for hunting ability in males may also have been partly sexual selection, if meat was exchanged for sex with females (i.e. if hunting was part of male mating effort). Hill and Hurtando (1996) found that among the Ache, modern hunter-gatherers in South America, there was a highly significant positive relationship between male fertility and hunting skill. Women's subsistence activities in contemporary foraging societies, such as gathering, are less dependent on physical strength (Murdock and Provost, 1973). One would expect females to be under different selection pressures, perhaps for earlier maturation or maximum energy efficiency (Andersson, 1994). It is hypothesised that the high levels of sexual size dimorphism observed in the Late Palaeolithic were a consequence of the different natural selection pressures on males and females during this period.

In the Mesolithic, there was a shift towards hunting smaller, less dangerous game, and also the invention of the bow and arrow, which reduced selective pressures on males for large size. Male size decreased, perhaps because a smaller body size requires less energy and protein for maintenance (Frayer, 1980; 1981). Sexual dimorphism was reduced as a consequence. With the advent of agriculture, there was probably a convergence of male and female subsistence activities. In modern agricultural populations, there is more overlap in male and female subsistence activities than in

hunter-gatherers (Murdock and Provost, 1973). Selection pressures on stature in males and females are therefore hypothesised to have converged, further reducing sexual dimorphism.

Archaeological evidence for a reduction in sexual dimorphism over time, coinciding with changes in subsistence, especially the advent of agriculture, varies across regions.

Europe. Frayer (1980; 1981) found that in Europe sexual dimorphism has declined since the Late Palaeolithic, through the Mesolithic and the Neolithic. Frayer (1980) calculated sexual dimorphism in stature by:

$$\frac{\text{mean male stature - mean female stature}}{\text{mean male stature}} \times 100$$

He found that sexual dimorphism in stature declined from 8.6% in the Late Palaeolithic, to 6.6% in the Mesolithic and to 5.9% in the Neolithic. Using data on stature in modern populations from Eveleth and Tanner (1976) he also showed that modern European populations are as tall as Palaeolithic populations, but less sexually dimorphic, indicating that the decline in sexual dimorphism since the Late Palaeolithic is not simply an allometric effect. Frayer (1980) found that the decline in sexual dimorphism between the Mesolithic and the Neolithic was associated with a relative increase in female stature. Frayer (1981) found that the decline in sexual dimorphism since the Late Palaeolithic was associated with decreasing male lower limb length.

In contrast, Meiklejohn et al. (1984), using a different sample, found that sexual dimorphism declined in Europe between the Late Palaeolithic and the Mesolithic, but increased in the Neolithic.

Asia. In the Levant, Smith et al. (1984) found no evidence of change in either sexual dimorphism or hunting behaviour between the Late Palaeolithic and the Neolithic. Kennedy (1984) found that in South Asia the advent of agriculture (from ca. 6500 BP) was associated with a decline in sexual dimorphism and stature, which he related to low protein intake in agricultural populations.

The Americas. In coastal Peru, Benfer (1984) found no evidence of decreased dimorphism in stature with the advent of agriculture (8000-4500 BP) but he did observe diminished sexual dimorphism in bony response to musculature. Larsen (1984) found that sexual dimorphism increased with the adoption of maize agriculture in coastal Georgia (ca. 1115 AD), associated with a relative decline in female stature. He argues that this may be because women cultivated maize, a low protein food, while men remained hunters. This pattern of sexual division of labour among populations with mixed maize farming and hunting in America is described in the ethnographic record (Murdock, 1967). Perzigian et al. (1984) also found that sexual dimorphism was greater among maize agriculturalists (ca. 700-1600 AD) than hunter-gatherers (before 1000 BC) in the Ohio River Valley. Cook (1984) found no changes in sexual dimorphism related to changes in subsistence in the Lower Illinois River Valley. Goodman et al. (1984) found no significant changes in sexual

dimorphism with the advent of maize agriculture at Dickson Mounds in Illinois (950-1300 AD).

Australia. Brace and Ryan (1980) reported a decrease in skeletal and dental robusticity and sexual dimorphism between Late Palaeolithic and modern hunter-gatherers. They related this to a decline in large game hunting. No specific decline in dimorphism in stature was reported.

Archaeological evidence has limitations for testing hypotheses about the causes of variation in sexual dimorphism. In many cases the hypothesis that changes in sexual dimorphism in archaeological populations are related to changes in subsistence is *post hoc*. The alternative hypothesis that sexual dimorphism is related to polygynous mating is not testable in archaeological populations, because marriage practices are not known. Many of the changes in sexual dimorphism with agriculture are inconsistent across populations. Other problems in the analysis of sexual dimorphism in archaeological populations include small samples of males and females from which to estimate sexual dimorphism, problems of sexing, and the difficulty of estimating stature from bones (Hamilton, 1982).

The sexual division of labour hypothesis can also be tested on ethnographic populations. Wolfe and Gray (1982b) tested whether contemporary agricultural populations are less sexually dimorphic than modern hunter-gatherers. They used a sample of 73 societies from the Standard Cross-Cultural Sample (Murdock and White, 1969) for which stature data for males and females was available. They found that agriculturalists were more sexually dimorphic than hunter-gatherers, contrary to

the prediction of the hypothesis. Again, similarities among populations were not adequately controlled for in this study. It is shown below that hunting and agriculture, like sexual dimorphism, are highly significantly associated with phylogeny.

Two aspects of the sexual division of labour might affect sexual dimorphism in stature. First, the effect of different *types* of subsistence on sexual dimorphism was tested. Is there is a positive relationship between sexual dimorphism in stature and reliance on hunting, a primarily male activity? Is there is a negative relationship between sexual dimorphism in stature and agriculture, an activity that is shared more equally between the sexes? Second, the overall sexual division of labour was calculated, and it was tested whether there is an association between sexual dimorphism in stature and the *amount* of work done by males and females in a population.

6.2.3 Absolute size, nutrition and secular change

Allometry. Across human populations, sexual dimorphism is positively associated with body size. This relationship is also observed across many groups of species, and is known as Rensch's rule (Abouheif et al., 1997). In humans, male stature is about 1.1 times greater than female stature. However, the aim of the present study was not to explore the allometric relationship between male and female stature in humans, but to investigate deviation from the underlying pattern. Sexual dimorphism was measured using residuals of the reduced major axis (see section 6.3.1) which ensures that there is no relationship between estimated sexual dimorphism and absolute body size (Ranta et al., 1994).

Nutrition. One hypothesised cause of variation in sexual dimorphism that could not be directly investigated here is nutritional status. Information about nutritional intake was lacking for most of the populations in the sample. It has been hypothesised that well-nourished populations are more sexually dimorphic than malnourished populations, because male growth is more susceptible to nutritional deficiencies during development than female growth (Hiernaux, 1968; Hamilton, 1982). A different developmental reaction norm to variance in nutritional intake in males and females could reflect different fitness consequences of variation in height for males and females. Hamilton (1982) reviews evidence that childbirth and lactation impose stabilising selection on female size in nutritionally stressed populations.

Although nutritional status may be one of several causes that affect sexual dimorphism in stature, it is unlikely to explain all cross-cultural variation in sexual dimorphism. Eveleth (1975) found that across continents African populations were the least dimorphic, but Native Americans were more dimorphic than Europeans, which is unlikely to be explicable in terms of better nutrition among Native Americans. I will argue below that the degree of sexual dimorphism may be determined by the *relative* nutritional status of boys and girls.

Secular change in stature. This study focuses on the long-term effects of the different traditional subsistence practices, not on the consequences of recent urbanisation and industrial development. Industrial populations have undergone a secular increase in stature in the past century (Eveleth and Tanner, 1990). This may increase sexual dimorphism, particularly in its early stages, because male growth is more sensitive to environmental conditions (Brauer, 1982). Populations from industrialised countries (Europe and Japan) were not included in the sample.

A literature review of secular changes in stature in the populations in the sample indicates that a positive secular trend was not a general feature of the populations in the sample at the date when the stature measurements were taken. This review covered only the years when the stature measurements in the sample were taken (mostly before 1970). A summary of patterns of secular change in populations in the sample, where known, follows. In Africa, no secular change in stature occurred in Bantu-speaking South Africans (ca.1919-1973) (Tobias, 1989) or in rural populations in Mali, West Africa (including the Fulani and Mossi, 1917-1985) (Prazuck et al., 1988). Secular increase in stature has been observed in the Kalahari San (from

ca.1900 to 1962) (Tobias, 1962). In Asia, a overall secular decline in stature has been observed in India over the years 1881 to 1963 (populations including the Toda, who experienced an increase in stature, and the Oraons and Bhil, who experienced a decrease in stature) (Ganguly, 1979). A secular increase in stature was observed in males but not in females in the Tungus, otherwise known as the Evenki (from ca. 1900 to1992) (Leonard et al., 1996). In America a secular increase in stature was observed in the Western Apache (1940-1967) by Miller (1970) but other studies indicate stable or decreasing stature decrease in Apache (1935-1961) and Navaho and Papago groups (early to mid-20th century) (Moore, 1972). No stature increase was observed in the Yucatec Maya (1895-1968) (McCullough, 1982). A secular increase in stature was observed in Australian Aborigines (1930-1970) (Barrett and Brown, 1971). Variable patterns of secular change were recorded in Papua New Guinea (ca. 1900 to 1981) (Ulijaszk, 1993). In Fiji a secular trend was seen in the years 1970-85, but not in the years 1930-70 (Clegg, 1989).

Tobias (1985) surveyed evidence of a secular trend in subsistence-level populations in the 20th century. He found evidence for a positive secular trend in hunter-gatherers but not generally not among agriculturalists. This pattern is also seen in the present sample (e.g. the !Kung and Australian Aborigines). Insofar as a secular increase in height also increases dimorphism (Brauer, 1982), the effect of the secular trend among hunter-gatherers would be to favour the hypothesis that sexual dimorphism is associated with hunting. No support was found for this hypothesis in the present analysis. It is concluded that secular changes in stature probably do not influence the results of this study.

I have ignored the question of whether cross-cultural variation in sexual dimorphism is a genetic trait, or an aspect of phenotypic plasticity. Rogers and Mukherjee (1992) argue that it is doubtful whether there has been sufficient time and stability in cultural behaviours for genetic variance in sexual dimorphism to evolve across populations. But the distinction between genetic and phenotypic traits does not greatly matter when investigating the adaptive value of a trait. Both phenotypic and genetic traits can be adaptive. Phenotypic plasticity is an adaptation which allows individuals to respond adaptively to their environment, in this case, during growth and development. The reaction norm of developmental response to the environment is heritable, although the resulting phenotype (e.g. stature) is a response to the environment.

6.3 Data

Data on stature were taken from a variety of published sources (see Table 6.1). Only samples that included at least 20 individuals of each sex were included. Further criteria for inclusion in the dataset were as follows. First, all populations are found in the *Ethnographic Atlas* (Murdock, 1967; n.d.). Stature samples were considered to come from cultures in the *Ethnographic Atlas* if they had the same name as a single culture (e.g. Zulu), or if they came from the same cultural 'cluster' (a group of similar cultures sharing a common ancestor within the past 1,000 years) and had the same geographical location as a single culture within the cluster. In the latter case, the

stature sample was assigned to the culture in that cluster which had the same geographical location. Any ambiguities in assigning stature samples to cultures in the *Ethnographic Atlas* are noted in Table 6.1. All cultures included in the dataset also had information about their means of subsistence, marriage practices and the sexual division of labour in the *Ethnographic Atlas.*

All populations in the sample are also included in Appendix 3 of *The History and Geography of Human Genes* (Cavalli-Sforza et al., 1994). This book includes information about the genetic relationships of hundreds of different populations worldwide. All populations included are aboriginal, defined as populations which inhabited their present location before 1492 (Cavalli-Sforza et al., 1994). Thus all American populations included in the current dataset are Native Americans, using the term to include Inuit (Eskimos) and South American Indians. As previously stated, populations from Europe and Japan were not included.

The criteria for inclusion outlined above resulted in a dataset of seventy-six populations, which are listed by continent (following Murdock's six geographical regions) in Table 6.1. The Totonac were excluded from the final analysis, because they had no data on marriage.

Table 6.1 Male and female stature in 76 populations worldwide, listed by geographical region.

Tables 6.1.1 to 6.1.6 show male and female stature in Africa, the Circum-Mediterranean, Asia, the Island Pacific and Australia, and North and South America. The ethnic group and *Ethnographic Atlas* (E.A) code of each sample is shown, together with the number of individuals sampled (n) and mean stature (Ht) for males and females. References for the stature samples are shown.

Table 6.1.1 Male and female stature Sub-Saharan Africa

		Males		Females		
Ethnic group	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
Ashanti	Af3	48	164.2	27	154.7	Rattray, 1923
Bamileke	Ae5	352	168.4	236	158.6	Hiernaux, 1968
Bamum	Ae50	71	171.5	58	163.1	Hiernaux, 1968
Basa	Ah11	90	167.9	52	159.2	Hiernaux, 1968
Duala	Ae12	75	169.1	50	156.9	Hiernaux, 1968
Ganda	Ad7	61	163.6	66	156.2	Eveleth and Tanner, 1976
"	"	261	167.3	242	156	Hiernaux, 1968
Hadza	Aa9	36	160.5	31	150	Eveleth and Tanner, 1976
Ibo	Af10	68	165.5	54	154.5	Hiernaux, 1968
Kikuyu	Ad4	412	163.6	100	151.6	Orr and Gilks, 1931
Maasai	Aj2	362	165.9	333	152.4	Orr and Gilks, 1931

"	"	88	171.2	180	159.9	Sellen, 1995
Mbuti (Eastern, or Ituri Pygmies)	Aa5	71	144.4	38	136.0	Cavalli-Sforza, 1986, or Eveleth and Tanner, 1990
"	"	510	144.0	382	137.0	Hiernaux, 1968
"	"	69	144.2	32	137.4	Cavalli-Sforza, 1986
Mossi (Haute-Volta)	Ag47	49	167.8	58	158.6	Froment and Hiernaux, 1984
	"	27	168.9	119	158.7	"
Nama	Aa3	73	162.4	27	149.7	Shapira, 1930
San ('Bushmen')	Aa1 (!Kung)[16]	292	159.4	346	150.0	Eveleth and Tanner, 1976
"	"	58	157.7	77	146.6	Hiernaux, 1968
"	"	22	159.3	22	148.8	Shapira, 1930
Turkana	Aj5	40	173.9	42	163.3	Sellen, 1995
Venda	Ab6	168	167.6	56	154.0	Hiernaux, 1968
Yoruba	Af6	340	167.5	205	155.0	Eveleth and Tanner, 1976
Zulu	Ab12	106	166.1	219	156.0	Eveleth and Tanner, 1976

16 Unclear from stature sources which group of San were studied. The !Kung are the largest population in Murdock's 'Bushman' (i.e. San) cluster. The Naron (an alternative possibility) are also hunter-gatherers with similar sexual division of labour and marriage practices.

Table 6.1.2 Male and female stature in the Circum-Mediterranean

		Males		Females		
Ethnic group	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
Algerians	Cd12	96	172.5	29	160.8	Eveleth and Tanner, 1976
Druze (Near East)	Cj8	181	165.6	114	152.2	Shanklin and Izzeddin, 1937
Egyptians	Cd2	-	171.6	-	159.2	Eveleth and Tanner, 1990
Fulani, or Peul	Cb8	42	172.7	41	161.7	Hiernaux, 1968
(Niger)	(Bororo)[17]	32	176.3	30	164.6	Sellen, 1995
Kurds (Iraq)	Ci11	598	166.1	31	152.7	Field, 1952
Nubians (mainly Kenuzi and Fedichi)	Cd1 (Kenuzi Nubians)	127	169.5	282	157.4	Valsik et al., 1970

[17] Located on the border of Niger and Nigeria.

Table 6.1.3 Male and female stature in Asia

		Males		Females		
Ethnic group	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
Bhil (India)	Ef5	56	158.8	46	149.5	Field, 1970 (p4 and 176)
Chukchi (Siberia)	Ec3	70	165.1	82	152.6	Smirnova, 1979
Khalka Mongols	Eb3	59	164.8	49	151.3	Eveleth and Tanner, 1976
Khasi (India)	Ei8	100	156.7	65	147.0	Field, 1970 (p201-3)
Koreans	Ed1	280	170.1	49	156.2	Eveleth and Tanner, 1976
Muria Gond (India)	Eg13	52	157.8	52	147.9	Field, 1970 (p3 and 176)
Oraons (India)	Ef6	100	160.4	110	149.4	Field, 1970 (p6 and 176)
Punjabis	Ea13 (West Punjabis)	-	168.3	-	155.8	Eveleth and Tanner, 1976
Toda (India)	Eg4	25	170.3	25	153.0	Field, 1970 (p21-22 and 176-
"	"	61	168.3	58	153.7	7)
"	"	82	169.8	25	155.6	"
"	"	73	171.9	39	157.7	"
Tungus	Ec9 (Goldi[18])	52	156.5	72	146.5	Skeller, 1954
Wood Nenetz (Siberia)	Ec4 (Yurak[19])	50	160.1	42	147.6	Smirnova, 1979

[18] Goldi are the only culture in Murdock's (1967) Tungus cluster. Tungus are known today as Evenki.
[19] Yurak is an ethnonym of Nenetz.

Table 6.1.4 Male and female stature in the Island Pacific and Australia

			Males		Females		
Region	**Ethnic group**	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
S.E. Asia - Taiwan	**Ami**	Ia9	146	164.6	94	155.9	Chai, 1967
"	**Atayal**	Ia1	96	160.1	147	149.8	Chai, 1967
"	**Banun**	Ia10	96	157.2	110	146.2	Chai, 1967
"	**Paiwan**	Ia6	127	156.6	150	148.0	Chai, 1967
S.E. Asia	**Javanese**	Ib2	-	158.0	-	150.0	Eveleth and Tanner, 1976
Pacific Islands	**Manus**	Ig9	20	162.9	20	151.0	Eveleth and Tanner, 1976
"	**Lau (Solomon Islands)**	Ih4	20	164	38	153.4	Eveleth and Tanner, 1990
"	**Ontong Java**	Ii5	75	166.2	119	156.0	Eveleth and Tanner, 1990
"	**Kwaio**	Ie13	46	161.0	49	149.7	Eveleth and Tanner, 1990
"	**American Samoa**	Ii1	468	171	698	160.6	Eveleth and Tanner, 1990
"	**Western Samoa**	Ii14	101	170.4	144	158.3	Eveleth and Tanner, 1990
Australia	**Australian Aborigines (mostly Walbiri)**	Id10	39	172.1	23	162.9	Eveleth and Tanner, 1990
Papua New Guinea	**Kiwai**	Ie13	25	168.3	25	157.3	Hyndman et al., 1989

Table 6.1.5 Male and female stature in North America

		Males		Females		
Ethnic group	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
Angmagsalik Inuit	Na24	166	162.0	203	153.3	Skeller, 1954
Apache	Nh11 (Western Apache)	31	168.4	46	153.3	Eveleth and Tanner, 1976
Blackfeet	Ne12	38	177.4	46	164.8	Eveleth and Tanner, 1976
Chippewyan	Na30	44	166.4	20	150.9	Skeller, 1954
Copper Inuit	Na3	82	164.8	42	156.4	Jenness, 1923
Greenland Inuit	Na25	500	162	400	152	Skeller, 1954
Iglulik Inuit	Na22	20	166	20	153.7	Jenness, 1923
Labrador Inuit	Na23	58	158.4	78	148.3	Skeller, 1954
Navaho	Nh3	90	169.6	33	154.2	Hrdlicka, 1935
Nootka	Nb11	33	168.7	42	158.2	Birkbeck and Lee, 1973
Papago	Ni2	50	170.9	30	155.9	Comas, 1971, or Hrdlicka, 1935
Pima	Ni6	53	171.8	30	157.4	Comas, 1971, or Hrdlicka,
"	"	77	169.6	51	156.3	1935
Tarahumara	Ni1	50	163	30	150.8	Comas, 1971
Tarasco	Nj8	50	163.1	30	150.8	Comas, 1971
"	"	111	161.8	157	151.2	"
Totonac[20]	Nj4	100	158.0	100	146.3	Comas, 1971
Zuni	Nh4	60	163.5	32	151.2	Hrdlicka, 1935

[20] The Totonac were excluded from the final analysis because the *Ethnographic Atlas* has no information on their marriage practices.

Table 6.1.6 Male and female stature in South America

		Males		Females		
Ethnic group	**E. A. code**	**n**	**Ht**	**n**	**Ht**	**Reference**
Alacaluf	Sg5	28	156.4	34	146.3	Steggarda, 1963
Aymara	Sf2	66	164.1	66	151.4	Eveleth and Tanner, 1990
"	"	45	160.0	69	149.6	"
"	"	70	163.0	90	150.0	"
"	"	62	159.9	58	148.1	"
"	"	57	163.1	60	149.8	"
"	"	25	162.0	39	149.0	"
Barama River Caribs	Sc3	104	156.8	99	145.8	Steggarda, 1963, or Gillen, 1936
Cayapo	Sj9	110	165.4	156	153.9	Eveleth and Tanner, 1976
Macusi	Sc12	42	156.8	28	146.3	Steggarda, 1963
Mataco	Sh1	30	163.8	20	152.9	Steggarda, 1963
Maya	Sa6	77	155.1	56	142.7	Comas, 1971
"	"	128	155.4	94	141.8	"
"	"	42	156.8	20	142.8	Eveleth and Tanner, 1976
Miskito	Sa9	30	164.0	32	154.0	Eveleth and Tanner, 1990
Quiche	Sa13	117	153.8	83	143.8	Comas, 1971
Toba	Sh8	190	167.8	212	157.7	Comas, 1971
Xavante	Sj11	42	170.2	39	156.3	Comas, 1971, or Eveleth and Tanner, 1976
Yanomama	Sd9	316	153.2	260	142.3	Eveleth and Tanner, 1976

Data on hunting and agriculture, as a percentage of total subsistence, were taken from the *Ethnographic Atlas* (Murdock, 1967). The *Ethnographic Atlas* also gives information on the sexual division of labour for five types of subsistence activity, gathering, hunting, fishing, pastoralism and agriculture (columns 54-62). These codes were adapted for use in this analysis as shown in Table 6.2. To estimate the overall sexual division of labour in each society, the percentage contributed by women to each type of subsistence activity was multiplied by the percentage contributed by that type of subsistence activity to total food production in that population. The overall proportion (per cent) of work done by women in each population was calculated by summing the contribution of women to each of the five types of subsistence activity.

When data on the sexual division of labour was missing, it was estimated from the average proportion of work done by women in that region. This applies to two cultures which had no data on the sexual division of labour for 20% of their total subsistence activities and thirteen cultures which had no data on the sexual division of labour for 10% of their total subsistence activities. The regions from which missing data on the sexual division of labour were estimated were sub-Saharan Africa, the Circum-Mediterranean, Asia, the Island Pacific, North America (above 40 degrees latitude), Central America (below 40 degrees latitude but north of Panama) and South America. With the exception of Asia each of these regions shows a clear pattern in the sexual division of labour, so missing data can probably be quite accurately estimated. The amount of work done by women in the present sample, across Murdock's six geographical regions, is shown in Table 6.3.

Table 6.2 Adaptation of the *Ethnographic Atlas* codes on women's work

Murdock's code	*Ethnographic Atlas* description	Estimated % women's work
M	Males alone perform the activity, female participation being negligible.	0
N	Both sexes participate, but males do appreciably more than females.	25
D	Differentiation of specific tasks by sex but approximately equal participation by both sexes in total activity.	50
E	Equal participation by both sexes without marked or reported differentiation in relation to sex.	50
G	Both sexes participate, but females do appreciably more than males.	75
F	Females alone perform the activity, male participation being negligible.	100
P	The activity is present, but sex participation is unspecified in the sources consulted.	Missing data

Table 6.3 Women's work across geographical regions

Five regions (Africa, the Circum-Mediterranean, Island Pacific and Australia, Asia and South America) follow Murdock (1967). North America is divided because women's work varies between the between the far north and centre of the continent. For each region the mean of women's work as a percentage of total subsistence work is shown, with the standard deviation.

Region	Number of cultures	Mean % women's work	S.D. % women's work
Sub-Saharan Africa	18	51.1	12.58
Circum-Mediterranean	6	21.7	5.9
Asia	11	27.3	18.42
Australia and Island Pacific	13	43.5	11.55
America (>40 degrees N)	8	11.25	12.25
America (Panama to 40N)	8	25.96	15.73
South America	12	33.5	15.38

The *Ethnographic Atlas* classifies marriage as polyandrous, monogamous, 'occasionally polygynous' (i.e. 'polygyny is occasional or limited'), or 'generally polygynous' (i.e. 'polygyny is common or general') (Murdock, 1967, column 14). In societies with limited or occasional polygyny, less than 20% of marriages are polygynous. General polygyny means that more than 20% of marriages are polygynous. From Murdock's codes, an ordinal scale of frequency of polygyny was formed. Monogamous populations were given a score of 1. Populations which practice occasional polygyny were given a score of 2. Populations where polygyny is common or general were given a score of 3. There were no polyandrous cultures in the sample. This ordinal scale was intended to measure the amount of competition for females experienced by males, which was assumed to be closely related to marriage norms in any particular society.

Marriage can also be scored as a two-state discrete character, either as 'generally polygynous' versus all other states, or 'any polygyny' versus 'no polygyny'. The comparative analysis carried out (below) was performed both with marriage as a discrete variable and an ordinal variable, and it made no difference to the results.

The geographical location of each population (where the main ethnographic study was done) was also taken from Murdock's (1967) *Ethnographic Atlas*. The geographical location of each population, together with marriage, hunting, agriculture and women's work (per cent total subsistence), are shown in Table 6.4.

Table 6.4 Geographical location of populations, sexual division of labour, and polygyny, listed by continent

Data are from Murdock (1967). In the column 3, a score of 1 indicates monogamy, 2 indicates that fewer than 20 per cent of marriages are polygynous, and 3 indicates that more than 20 per cent of marriages are polygynous. Hunting and agriculture are the percentage of total subsistence produced by these types of subsistence activity. Women's work is the percentage of all subsistence done by women.

Table 6.4.1 Circum-Mediterranean

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
Algerians	31N 2E	2	0	70	15
Druze	33N 35E	1	0	90	25
Egyptians	25N 33E	2	0	60	22.5
Fulani (Bororo)	13N 5E	3	0	20	30.18
Kurds	32N 44E	2	0	50	22.5
Nubians (Kenuzi)	23N 33E	2	0	60	15

Table 6.4.2 Sub-Saharan Africa

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
Ashanti	7N 2W	3	10	70	35
Bamileke	5N 10E	3	10	80	65.09
Bamum	6N 11E	3	10	70	65
Basa	8N 8E	3	10	60	40
Duala	4N 10E	3	0	60	57.59
Ganda	1N 32E	3	10	70	52.5
Hadza	3S 35E	2	40	0	60
Ibo	6N 7E	3	0	90	67.5
Kikuyu	1S 37E	3	0	70	52.5
Maasai	2S 36E	3	10	0	45
Mbuti	2N 28E	2	70	0	47.5
Mossi	12N 2W	3	10	60	40
Nama	26S 18E	2	30	0	35
San (!Kung)	20S 21E	2	20	0	60
Turkana	4N 35E	3	10	40	75
Venda	23S 30E	3	10	60	50.04
Yoruba	8N 4E	3	0	80	35.09
Zulu	29S 31E	3	10	50	37.5

Table 6.4.3 Asia

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
Bhil	22N 74E	2	10	50	30
Chukchi	66N 177E	3	20	0	12.5
Khalka Mongols	46N 97E	1	10	10	40
Khasi	26N 92E	1	10	50	57.5
Koreans	35N	1	0	60	35
Muria Gond	20N 81E	2	20	50	25
Oraons	23N 85E	2	0	70	42.5
Punjabis	32N 73E	1	0	80	5
Toda	12N 77E	1	0	0	10
Tungus	47N 132E	2	30	20	43.30
Wood Nenetz	68N 75E	2	30	0	0

Table 6.4.4 Australia and the Island Pacific

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
American Samoa	14S 170W	2	0	60	50
Ami	22 121	1	10	70	37.5
Atayal	24N 121E	1	20	60	55
Australian Aborigines (Walbiri)	22S 132E	3	40	0	60
Banun	24N 121E	1	30	60	55
Javanese	7S 110E	2	0	80	45
Kiwai	9S 143E	2	20	50	35
Kwaio	10S 143E	2	20	50	35
Lau	18S 179E	3	0	50	32.5
Manus	2S 147E	2	0	0	30
Ontong Java	10S 142E	3	0	50	50.5
Paiwan	22N 121E	2	20	60	55
Western Samoa	14S 172E	2	0	60	24.64

Table 6.4.5 North America

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
Angmagsalik Inuit	66 –37	2	20	0	0
Apache (Western)	36N 106W	1	10	80	2.54
Blackfeet	51N 112W	3	80	0	20
Chippewyan	60N 105W	2	60	0	0
Copper Inuit	69N 110W	1	40	0	15
Greenland Inuit	69N 53W	1	20	0	7.5
Iglulik Inuit	70N 82W	2	50	0	12.5
Labrador Inuit	58N 65W	2	40	0	0
Navaho	37N 110W	3	10	40	45
Nootka	49N 126W	2	20	0	35
Papago	31N 112S	3	20	50	42.5
Pima	31N 111W	2	10	50	30.04
Tarahumara	28N 107W	2	10	50	25
Tarasco	19N 101W	2	10	70	5.08
Totonac	20N 97W	Missing data	10	60	35
Zuni	35N 109W	1	10	80	22.54

Table 6.4.6 South America

Geographical location of populations, hunting and agriculture, sexual division of labour and polygyny.

Culture	Location	Marriage	Hunting (%)	Agriculture (%)	Women's work (%)
Alacaluf	52S 74W	2	20	0	38.92
Aymara	16S 69W	1	0	60	52.5
Barama River Caribs	5N 59W	2	20	40	40
Cayapo	8S 52W	1	20	60	40
Macusi	4N 59W	2	20	50	41.42
Mataco	24S 63W	2	20	10	32.5
Maya	18N 90W	1	10	70	0
Miskito	13N 85W	2	20	20	42.54
Quiche	15N 91W	2	0	90	5
Toba	25S 60W	2	30	30	38.92
Xavante	14S 52W	3	30	20	37.5
Yanomama	2N 65W	3	0	90	32.5

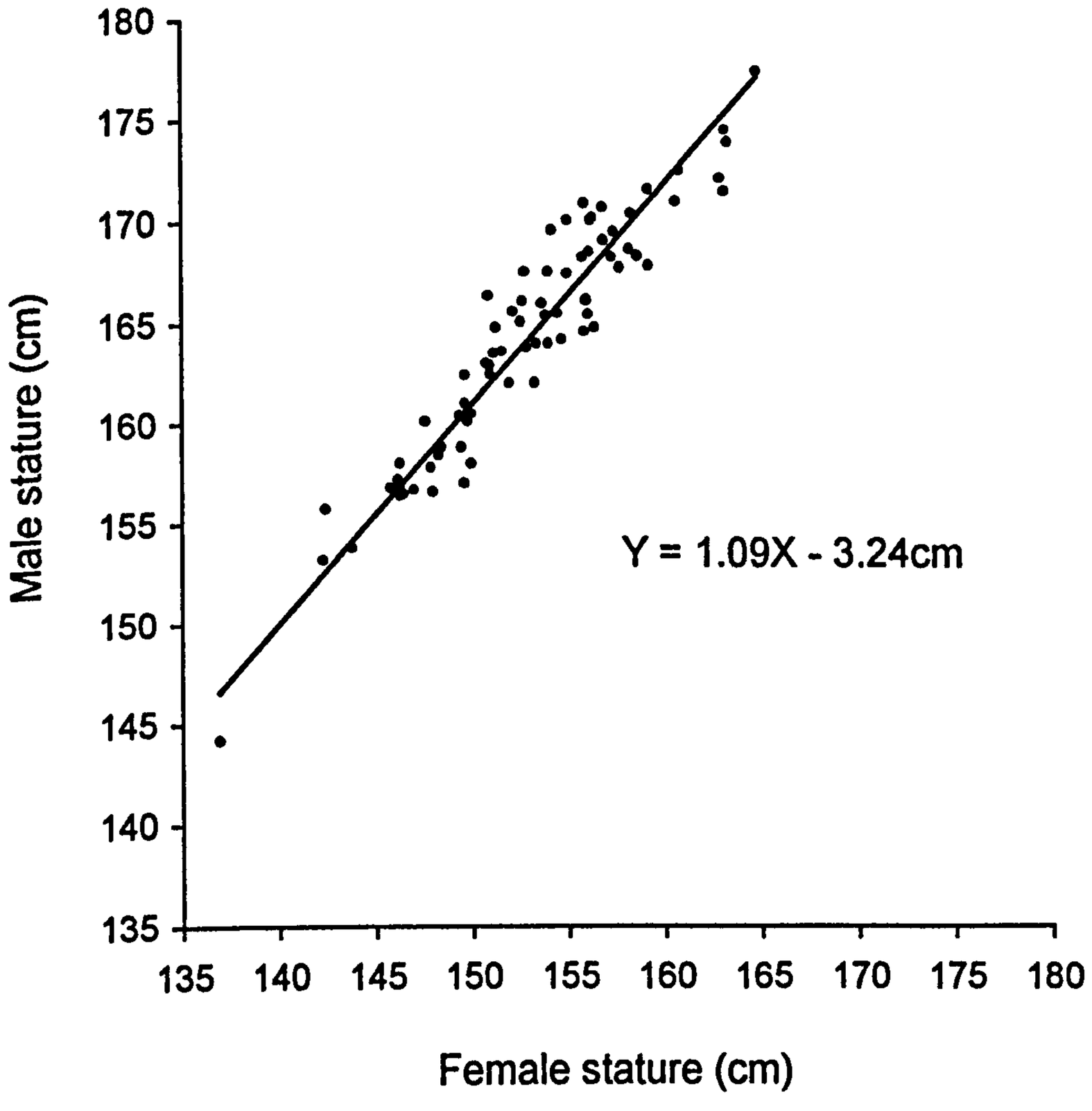
6.4 Statistical analysis and results

6.4.1 Measuring sexual dimorphism

Cross-cultural variance in sexual dimorphism was measured using residuals of the reduced major axis (Fig. 6.1). The reduced major axis, or Type II model, was used because both male and female stature estimates have a degree of associated error (Harvey and Mace, 1982). Previous studies of cross-cultural variance in sexual dimorphism used ratios of male to female stature to measure dimorphism (Alexander et al., 1979; Gray and Wolfe, 1980; Wolfe and Gray, 1982a; Gaulin and Boster, 1992). However residuals were used in the present analysis because for allometric traits (like dimorphism in stature) the size of ratios is not independent of body size. In humans, the ratio of male height to female height increases with body size (Gaulin and Boster, 1985; Ranta et al., 1994). Using residuals controls for the effect of body size, allowing one to determine which populations are less or more sexually dimorphic than expected for a given body size.

Figure 6.1 The relationship between male and female stature in 76 populations

The line fitted is the reduced major axis; residuals from this line were used to measure cross-cultural variation in sexual dimorphism.



Results. Mean male stature in the sample ranged from 144 cm in the Mbuti to 177 cm in the Blackfeet. Mean female stature ranged from 137 cm in the Mbuti to 165 cm in the Blackfeet. Male stature ranged from 4-10% larger than female stature. The relationship between male and female height, fitting the reduced major axis is:

male height = 1.09 (female height) – 3.24 cm.

This level of variation in sexual dimorphism in stature is comparable to that found in previous studies. The coefficient of determination (r^2) of the reduced major axis of male stature on female stature was 0.89, i.e. 89 % of the variance in male stature is 'explained' by the variance in female stature, leaving 11 % of the variance in male stature to be accounted for by other factors. The regional distribution of this variance showed a similar pattern to that found by Eveleth (1975). Africans were the least dimorphic populations, Asians showed intermediate dimorphism and Native Americans were the most dimorphic populations.

6.4.2 The transmission of biocultural traits

Aim. The aim of this part of the analysis was to investigate whether the biocultural variables tested are transmitted vertically or horizontally, or both, using the method described in chapter 3.

Statistical methods. Phylogenetic relatives were defined as the sister-group of each population on a genetic tree. The genetic tree used is shown in Figure 6.2, and

described further in section 6.3.3. Most populations could be compared to a single other population, with which they formed a paired clade at the tips of the tree (e.g. the Kikuyu and Ganda). In cases where three or more daughter populations descended from a single node (e.g. the Pima, Papago and Zuni), each population was compared to all the other populations in the clade. The mean value of each trait in the other populations in the clade was used. In some cases (e.g. the Mbuti) a population was co-ordinate with a larger clade. In these cases the population was compared to all populations in the co-ordinate clade. Again the mean value of each trait for all the other populations in the co-ordinate clade was used.

Nearest geographical neighbours were found using great-circle distances. Each population was compared to the same number of phylogenetic relatives and geographical neighbours. Thus, populations which were compared to a single phylogenetic relative were also compared to a single geographical neighbour (the nearest population). Populations compared to two or more phylogenetic relatives were compared to an equal number of their nearest geographical neighbours. Where populations were compared to more than one geographical neighbour, the mean of value of each trait in all geographical neighbours was used. The geographical locations of the populations in the sample are shown in Figure 6.3.

Multiple regression was used to test for an association between each trait in the populations in the sample (the dependent variable) and in their phylogenetic relatives and geographical neighbours (the independent variables). Five multiple regressions were performed, one for each variable whose transmission was tested. These included the degree of sexual dimorphism, women's work as a percentage of total subsistence,

hunting, agriculture, and amount of polygyny.

Results. Four out of five traits showed a highly significant association with phylogeny (phylogenetic relatives), including degree of sexual dimorphism, hunting, agriculture, and polygyny. Women's work had a marginally significant association with phylogeny. Two traits also showed an association with geographical neighbours, women's work and agriculture. The degree of sexual dimorphism had a marginally significant association with geographical neighbours. These results are shown in Table 6.5.

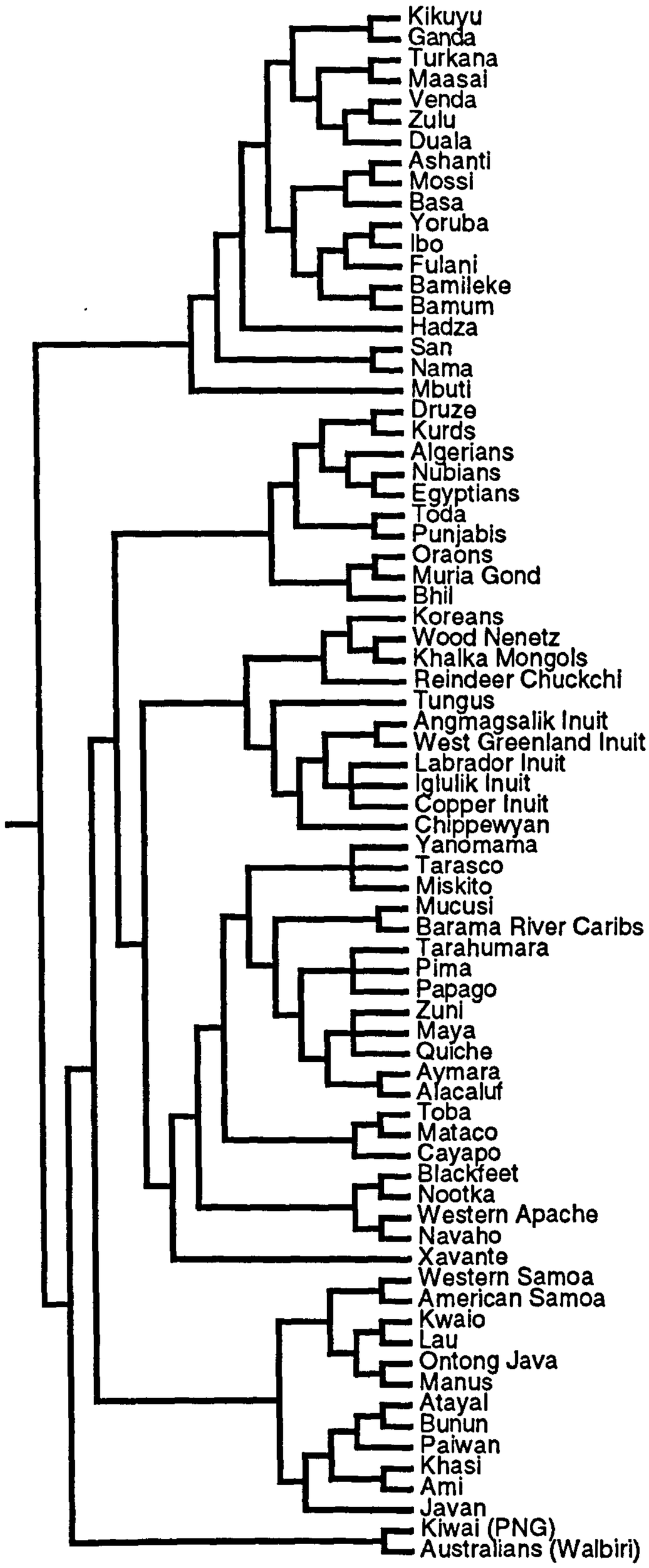


Figure 6.2 Genetic tree of 76 populations sampled for stature, adapted from Cavalli-Sforza et al.'s (1994) F_{ST} genetic trees.

Figure 6.3 Seventy-six populations worldwide, sampled for stature

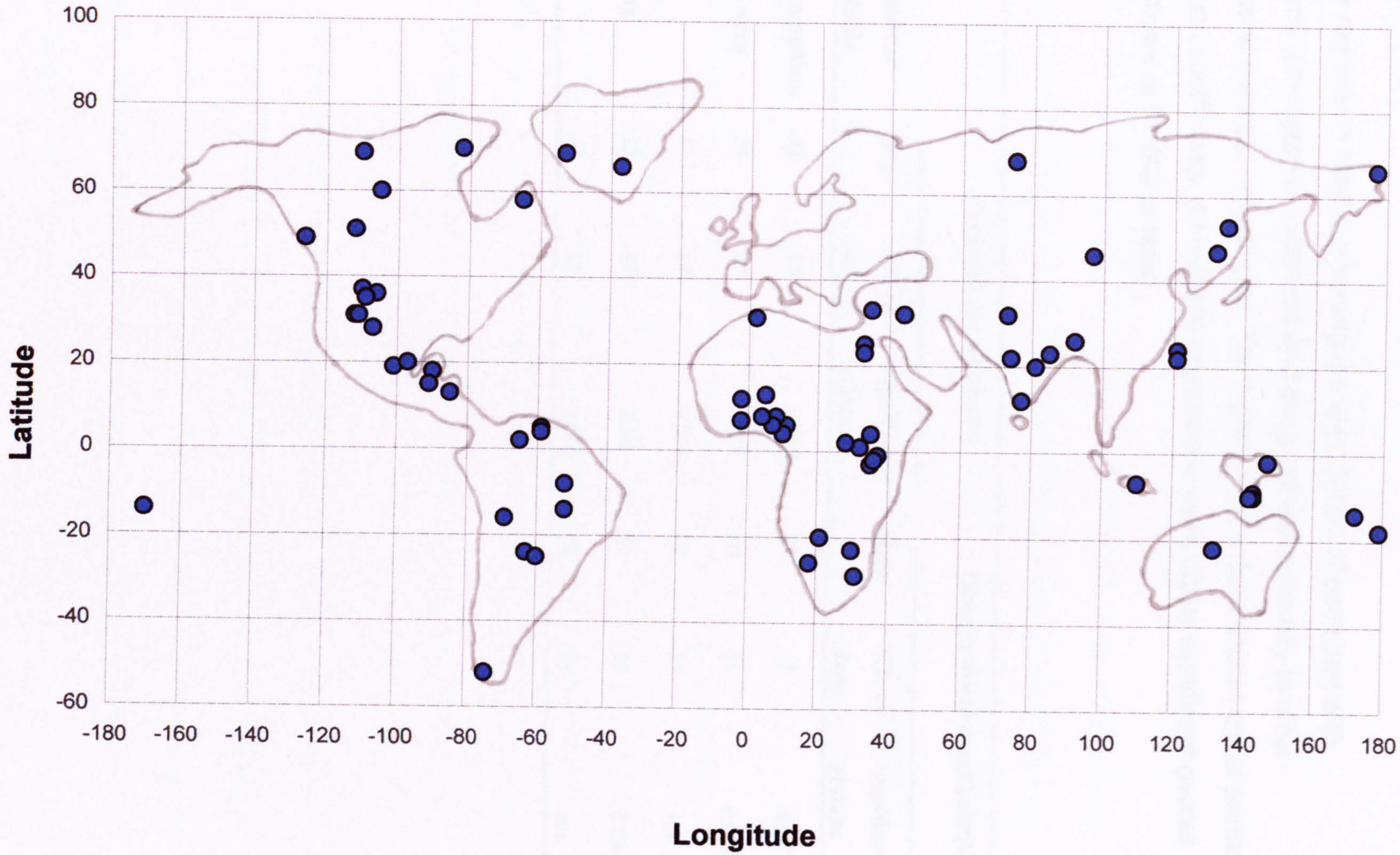


Table 6.5 The transmission between populations of biocultural traits

Multiple regression results, showing the association of each trait with phylogeny (phylogenetic relatives) and geographical proximity to other populations (nearest neighbours). The significance values shown are of partial regression coefficients. All multiple regressions were highly significant overall (F significant at 0.0002 or less).

	Phylogenetic relative(s)			Geographical neighbour(s)		
Dependent variable	**Slope**	**S.E. of slope**	**Significance of slope**	**Slope**	**S.E. of slope**	**Significance of slope**
Sexual dimorphism	.41	.13	0.002	.27	.15	0.07
Women's work	.24	.13	0.07	.50	.15	0.002
Hunting	.45	.17	0.008	.12	.15	**n.s.**
Agriculture	.33	.13	0.01	.33	.15	0.03
Polygyny	.42	.15	0.005	.14	.15	**n.s.**

6.4.3 A phylogenetic comparative test of the hypotheses

Statistical methods. Felsenstein's (1985) method of comparative analysis using independent contrasts was used to control for the effect of non-independence among populations. Two different trees were used to estimate phylogeny, to ensure that any effects found were not an artefact of a particular tree. The first tree was a genetic tree taken from Cavalli-Sforza et al., (1994), shown in Figure 6.2. It is a composite tree based on Cavalli-Sforza et al.'s (1994) F_{ST} genetic distance trees. Higher nodes follow Cavalli-Sforza et al.'s world tree (Fig. 2.3.2.B: Cavalli-Sforza et al., 1994:78). Lower nodes follow their genetic trees for individual continents or sub-continental regions (Figs. 3.5.1, 4.10.1, 4.11.1, 4.13.1, 4.14.1, 4.15.4, 6.9.1, 6.10.1, 6.10.3, 7.8.1, Cavalli-Sforza et al., 1994). Where there were conflicts among the source trees in Cavalli-Sforza et al., the tree in which populations were distinguished at a lower level was used. Seventy independent contrasts were generated from the genetic tree.

A second tree was a language tree. The language tree used follows Ruhlen (1991), assuming a monophyletic origin of languages. Fifty-one independent contrasts were generated from the language tree. This is lower than the number of contrasts from the genetic tree because the language tree is less resolved, especially among higher nodes. The language tree is shown in Figure 6.4.

Independent contrasts were generated after the method of Felsenstein (1985) and Pagel (1992), implemented by the computer program CAIC (Purvis and Rambaut, 1995). Correlated evolutionary change in sexual dimorphism and the other variables (polygyny, hunting, agriculture and women's work) was investigated using multiple regression, using SPSS. The dependent variable was independent contrasts in sexual dimorphism (residuals of the reduced major axis of male stature and female stature). The independent variables were independent contrasts in women's work, polygyny, hunting and agriculture. The regression is through the origin because independent contrasts are a measure of differences among sister populations, not actual character values (Pagel, 1992). Unresolved nodes were resolved on women's work because it was the most important independent variable.

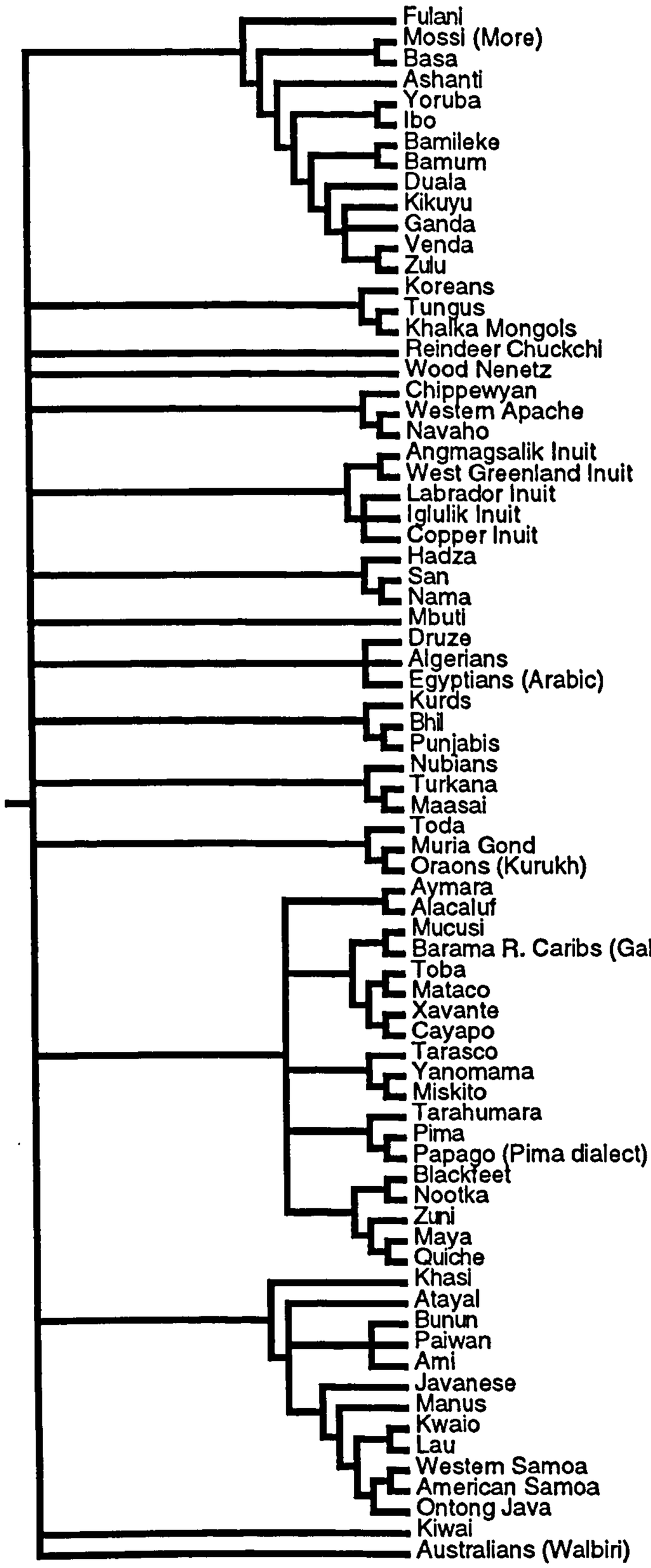


Figure 6.4 Linguistic tree of 76 populations sampled for stature, adapted from Ruhlen (1991), assuming a monophyletic origin of language.

Results. Independent contrasts in sexual dimorphism (residuals of the reduced major axis of male stature on female stature) are negatively associated with women's work (as a percentage of total subsistence labour). There was no relationship between independent contrasts in sexual dimorphism and polygyny, or between sexual dimorphism and either hunting or agriculture. These results are shown in Table 6.6.

Sexual dimorphism and the sexual division of labour are shown, mapped onto the genetic tree, in Figures 6.5 and 6.6. The sexual division of labour is clustered on the phylogeny (although it appears to be transmitted mainly horizontally, see section 6.4.2). The proportion of work done by women is relatively high in sub-Saharan Africa, and low in North Africa, Middle East, parts of India, north Asia, and northern and central America. Sexual dimorphism also clusters non-randomly with respect to phylogeny. Sexual dimorphism is relatively low in most sub-Saharan Africa, the Island Pacific and Australia. It is high in North Africa, the Middle East, parts of India, North Asia and north central America.

It is of interest to ask whether changes in the sexual division of labour affect male or female stature or both. To answer this question, two additional multiple regressions were performed, testing the effect of changes (contrasts) in women's work on male and female stature separately. Both male and female stature appear to be affected by the proportion of work done by women, although they are affected in different directions. Contrasts in mean stature in the two sexes are highly significantly associated. In addition, contrasts in male stature are negatively associated with contrasts in women's work, while contrasts in female stature are positively associated with contrasts in women's work. These results are shown in Tables 6.7 and 6.8.

Table 6.6 Regression of contrasts in sexual dimorphism on women's work

Multiple regression results of independent contrasts on the genetic and language trees. The dependent variable is independent contrasts in sexual dimorphism (residuals of the reduced major axis of male and female stature). Independent variables are independent contrasts in amount of women's work, hunting, agriculture and polygyny.

	Overall regression model			**Independent variable: women's work**		
Tree	**Multiple R**	**Adjusted R^2**	**F**	**Slope**	**S.E. slope**	**Significance**
Genetic tree	.28	.08	6.07	-.031	0.013	0.02
Language tree	.40	.16	9.65	-.042	0.013	0.003

Variables not in the equation: hunting, agriculture and polygyny.

Table 6.7 Regression of contrasts in male stature on female stature and women's work

Significance of overall multiple regression <0.0001.

Relationship between men's stature and independent variables

	Women's stature			Women's work (%)		
Tree	**Slope**	**S.E. slope**	**Significance**	**Slope**	**S.E. slope**	**Significance**
Genetic tree	1.041	.045	<0.0001	-.029	0.013	0.02
Language tree	1.057	0.053	<0.0001	-.041	0.014	0.004

Table 6.8 Regression of contrasts in female stature on male stature and women's work

Significance of overall multiple regression <0.0001.

Relationship between women's stature and independent variables

	Men's stature			Women's work (%)		
Tree	**Slope**	**S.E. slope**	**Significance**	**Slope**	**S.E. slope**	**Significance**
Genetic tree	0.85	0.037	<0.0001	0.029	0.011	0.01
Language tree	0.84	0.042	<0.0001	0.036	0.012	0.005

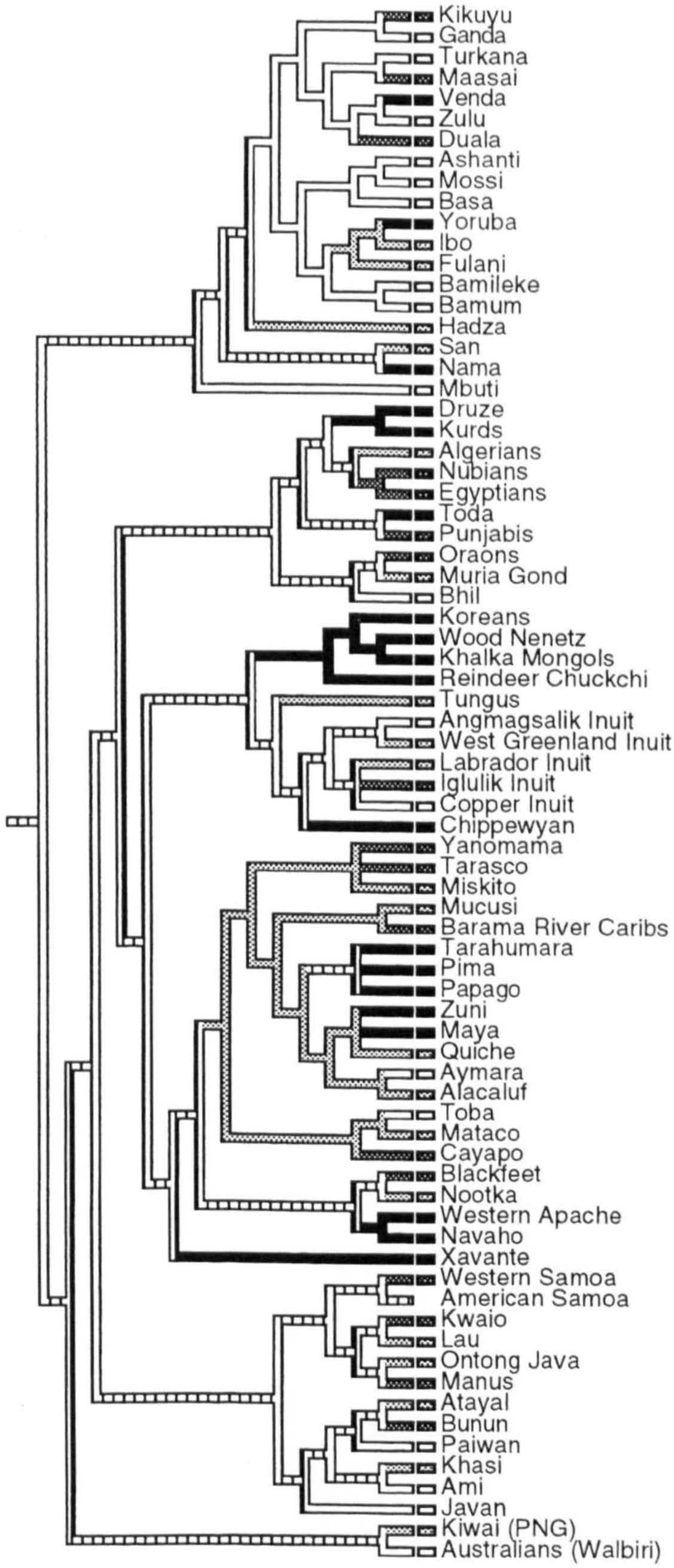


Figure 6.5 Sexual dimorphism in the sample, divided into quartiles for illustrative purposes, mapped onto the genetic tree. Black indicates the top quartile (the most dimorphic populations), dark and light grey show decreasing dimorphism (the second and third quartiles), white populations are the least sexually dimorphic.

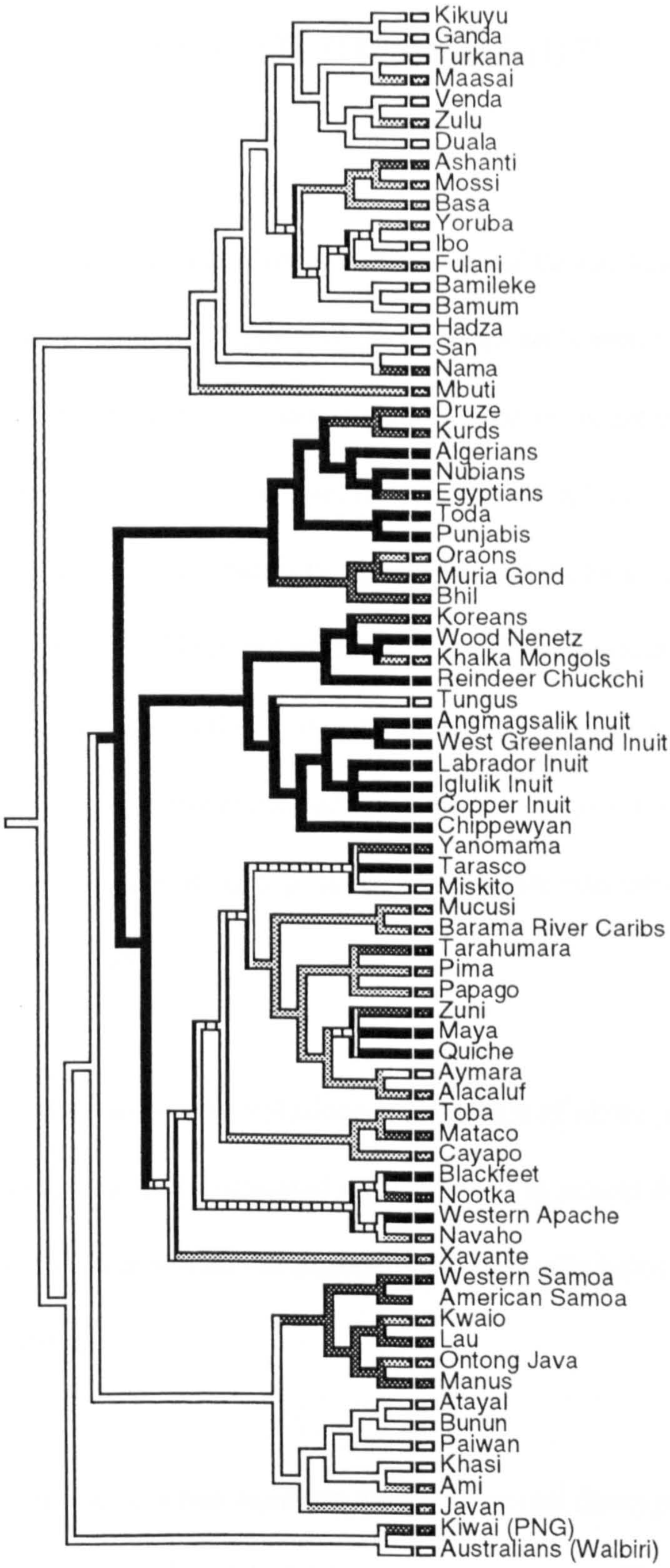


Figure 6.6. The proportion of subsistence work done by women, divided into quartiles, mapped onto the genetic tree. White shows the top quartile (the highest level of women's work), light and dark grey show a decreasing proportion of women's work (the second and third quartiles), black indicates populations with the lowest level of women's work.

6.5 Conclusions and discussion

In the analysis of the transmission of traits between populations, sexual dimorphism, polygyny, the sexual division of labour, and dependence on hunting and agriculture were associated with phylogeny. This indicates that these traits are inherited vertically, from 'mother' to 'daughter' populations. It is therefore essential to control for similarity due to inheritance when investigating correlations among these traits in a cross-cultural comparison. Three out of the five variables (women's work, variation in sexual dimorphism and agriculture) showed an additional association with geographical proximity. This indicates that these traits are also transmitted horizontally, between neighbouring populations, and/or are adaptations to similar geographical environments.

In the comparative analysis of the evolutionary correlates of sexual dimorphism, women's work was found to be correlated with variance in sexual dimorphism. There was no association between sexual dimorphism and particular types of subsistence, i.e. hunting or agriculture.

The negative association between women's work and sexual dimorphism in stature may result from cross-cultural variation in parental sex biases, affecting childhood nutrition, associated with variation in the overall sexual division of labour. Parental investment theory predicts that parents should invest more in offspring of one sex when that investment increases the parent's own inclusive fitness (Clutton-Brock, 1991). Children who act as 'helpers at the nest', who are engaged in food production

which benefits their parents or siblings, may receive more parental investment. Where males perform all or most subsistence labour, it may be adaptive for parents to invest more resources in their sons than daughters, insofar as the returns to parents (in terms of food production by children) are greater for sons than daughters. As a result, males would achieve a greater proportion of their potential adult stature than females. Sexual dimorphism would increase as a consequence. Conversely, in societies where females perform a large proportion of subsistence labour, parents may invest relatively more in their daughters, so that girls' growth is not compromised relative to boys' growth. Sexual dimorphism would therefore be diminished.

The greater value of male children in household production is often cited both by researchers and parents as a reason for male-biased parental investment (Arnold and Zhaoxiang, 1987; Bairagi, 1986; Levine, 1987; Smith and Smith, 1994; however c.f. Das Gupta, 1987 for an opposing view). Sex biases in parental investment are known to affect children's nutritional status, which in turn affects adult stature. There is good evidence from some South Asian populations that parental discrimination against girls can involve feeding them less both in quantity and quality of food (Bairagi, 1986; Chen at al., 1981; Levine, 1987; Das Gupta, 1987). This results in greater levels of malnutrition (affecting growth) among girls, as well as higher female child mortality rates (Chen at al., 1981; Bairagi, 1986). Discrimination against girls is not a universal pattern, however. In some parts of Africa, for example, girls are consistently found to be better nourished than boys (Quinn et al., 1995; Madise and Mpoma, 1997). It is suggested here that these variations in sex-bias in parental investment may be related to the greater contribution of females to subsistence in sub-Saharan Africa compared to Asia and Native America. Regional variation in women's work shows an

inverse pattern to variance in sexual dimorphism across regions. Women's work is highest in sub-Saharan Africa and lowest in North America and the Circum-Mediterranean (Table 6.3). Sexual dimorphism is lowest in sub-Saharan Africa and highest in Native America (Figure 6.5).

Sex biased juvenile mortality also shows the same geographical patterns as variation in sexual dimorphism. Male juvenile mortality is 'normally' expected to be higher than female juvenile mortality, because males are biologically more vulnerable than females. However, higher female than male child mortality is observed in regions where women contribute relatively little to subsistence, including South and East Asia (Das Gupta, 1987; Bairagi, 1986; Arnold and Zhaoxiang, 1986), and historically in the North American Inuit (Smith and Smith, 1994). Kishor (1993) found that female-biased infant and child mortality was associated with low participation by women in the labour force in India. In a cross-cultural study, Hewlett (1991) found that female-biased juvenile mortality was strongly statistically associated with a high male contribution to subsistence, as a consequence of male-biased parental investment in these societies. In Sub-Saharan Africa, where women contribute more to food production, higher than expected male juvenile mortality is observed in some populations (Cronk, 1989; Harpending and Pennington, 1991).

The type of subsistence activity, i.e. the amount of hunting or agriculture, showed no association with sexual dimorphism in stature. Sexual dimorphism in stature appears to be related to the overall sexual division of labour, but not to the kind of work (hunting or agriculture) done.

This may be contrasted with Frayer's (1980) and Brace and Ryan's (1980) hypothesis that the large sexual dimorphism of the late Pleistocene was associated with the large-game hunting economy. However, modern hunter-gatherers differ from Palaeolithic hunter-gathers in many respects and so the absence of any effect of hunting on sexual dimorphism among modern populations does not falsify Frayer's (1980) and Brace and Ryan's (1980) model. In particular, many modern hunter-gatherers such as the !Kung San and the Australian Walbiri inhabit more marginal habitats than Late Pleistocene hunters, and pursue a broader foraging economy where gathering and small game are more important than large game. In the foraging economies of modern hunter-gatherers there may be no selection for large body size in male hunters. For example, Hill and Hurtando (1996) found that males with medium body size were the best hunters in the Ache, contemporary South American hunter-gatherers. However, the sample used here also includes Inuit populations, in which large game hunting was a primary subsistence activity. It is concluded that in contemporary humans, neither hunting nor agriculture has any effect on sexual dimorphism. It is the amount of subsistence work done by men and women, rather than the type of subsistence practised, which has an effect on sexual dimorphism in different societies.

There was no support for the hypothesis that cross-cultural variance in sexual dimorphism in stature is associated with polygyny. But there are several reasons to suspect that this might be a Type II error (failure to detect a real effect). Placing marriage practices on a phylogeny reveals that 'general polygyny' is a highly clustered trait, mainly confined to agro-pastoralists in sub-Saharan Africa (Fig. 6.7). The number of independent contrasts in this trait is small, increasing the likelihood of not detecting a real association in the data. This does not mean that Felsenstein's

(1985) method of comparative analysis by independent contrasts lacks statistical power. Rather, this method reveals the real lack of independent cases on which this hypothesis can be tested.

It is also difficult to obtain accurate data on paternity and variance in male reproductive success, which may be only roughly correlated with marriage practices. Available data on marriage practices are also not ideal. Murdock's (1967) marriage codes are rather crude categories, classifying all cultures in the sample into only three groups (no polygyny, low polygyny and general polygyny). A quantitative estimate of the proportion of polygynous marriages in each population would be preferable. This would also increase the number of independent contrasts, increasing the probability of detecting any association between marriage practices and degree of sexual dimorphism.

However, from the available comparative data, it is concluded that cross-cultural variance in dimorphism is not associated with variation in marriage practices or sexual selection. In this respect cross-cultural variation in size dimorphism in humans differs from variance in size dimorphism across species in primates and other mammalian groups, which is thought to result from sexual selection (Alexander et al., 1979; Leutenegger, 1982).

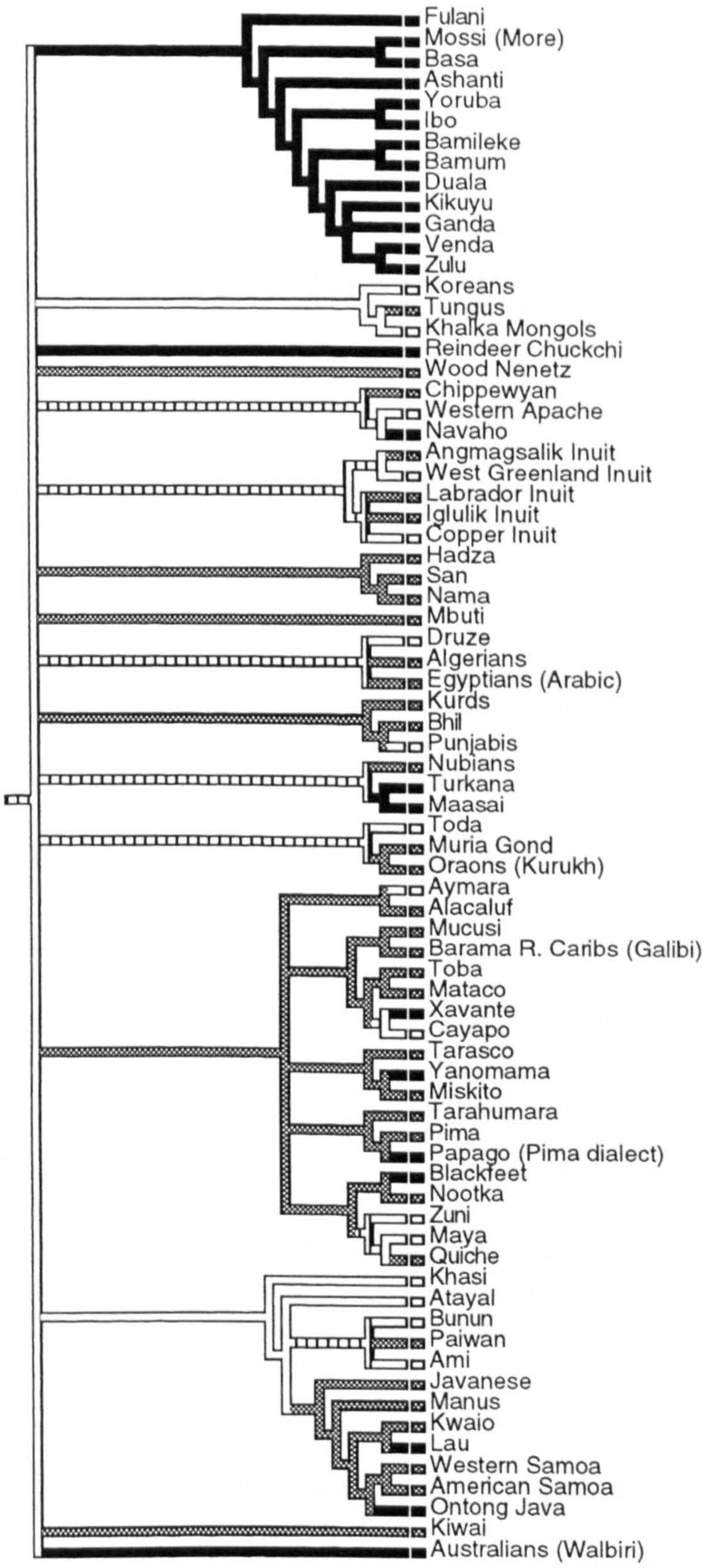


Figure 6.7 Marriage practices in populations mapped onto the language tree using parsimony (Maddison and Maddison 1994). Black=general polygyny, grey=occasional polygyny, white=no polygyny. Hatched lines indicate ambiguous ancestral states. Niger-Kordofanian speakers in this sample (at the top of the page) are all generally polygynous.

Chapter 7

Conclusions and general discussion

Conclusions to the individual case studies, testing hypotheses for cross-cultural variation in lactase persistence, wealth inheritance in Africa and sexual dimorphism, were discussed in chapters 4, 5 and 6. Here, general issues in phylogenetic comparative analysis in anthropology will be discussed.

Using models in anthropology. Throughout this thesis I have attempted to use explicit models of the past relationships among populations, and of the transmission of traits between populations. Making one's assumptions as explicit as possible in a model tends to reveal inadequacies in the model. This is of course an advantage, not a disadvantage, because it highlights where the model can be improved.

Tree models of past relationships among populations. Assumptions about the relationships between populations are always implicit in a comparative analysis, even if they are not made explicit. For example, in a standard cross-population comparison, an implicit assumption is that the populations in the sample are equidistantly related, i.e. in a star phylogeny (Felsenstein, 1985; Pagel and Harvey, 1989). Although one is

often uncertain which phylogeny best represents the past relationships among human populations, genetic and linguistic trees provide a better estimate of the hierarchical relationships among populations than a star phylogeny. Unresolved nodes and inconsistencies between different trees highlight our lack of knowledge about the past relationships among populations, showing where new data should be gathered. A task for the future is the development of models of population history that incorporate anastomoses (admixture) and porous boundaries between populations.

Results of the investigation into the transmission of traits between populations. The investigation of the transmission of biocultural traits among populations demonstrates the necessity of controlling for phylogeny in cross-cultural comparison. The inter-population transmission of most bio-cultural traits tested appears to be predominantly vertical, resembling the inheritance of traits between chronological species. Geographical diffusion appears to be less important than vertical inheritance for most traits. The strong phylogenetic signature of most bio-cultural traits suggests that their transmission from generation to generation is fairly conservative. Galton's problem is expected to affect these traits, whether or not they are phylogenetically constrained. The results of the analysis of the transmission of biocultural traits between populations are summarised in Table 7.1.

Table 7.1 The transmission of traits between populations, summary of results

Regression models showing association of traits with phylogenetic or linguistic relatives, and with an equal number of neighbouring populations (chapters of original analyses shown in column 1). The significance values shown are of partial regression coefficients. For logistic regression results, a negative coefficient indicates a positive relationship between the independent and dependent variables. All regression models were highly significant overall (for multiple regressions, F significant at <0.0002; for logistic regressions, chi-square log-likelihood significant at <0.0002).

Dependent variable	Phylogenetic or linguistic relative(s)			Geographical neighbour(s)		
	Multiple regression results (continuous variables)					
	Slope	**S.E. of slope**	**Significance of slope**	**Slope**	**S.E. of slope**	**Significance of slope**
High LDC (4)	.40	.16	0.02	.39	.19	0.05
Aridity (4)	.48	.16	0.004	.30	.20	**n.s.**
Solar radiation (4)	.34	.12	0.01	.84	.15	<0.0001
Pastoralism (4)	.63	.13	<0.0001	.15	.16	**n.s.**
Pastoralism (5)	.69	.08	<0.0001	.70	.10	0.06
Polygyny (5)	.78	.08	<0.0001	.18	.08	0.03
Sexual dimorph. (6)	.41	.13	0.002	.27	.15	0.07
Women's work (6)	.24	.13	0.07	.50	.15	0.002
Hunting (6)	.45	.17	0.008	.12	.15	**n.s.**
Agriculture (6)	.33	.13	0.01	.33	.15	0.03
	Logistic regression results (categorical variables)					
	Estimated coefficient	**S.E. of coefficient**	**Significance (Wald test)**	**Estimated coefficient**	**S.E. of coefficient**	**Significance (Wald test)**
Matrilineal inherit. of land (5)	-1.51	.35	<0.0001	-.17	.44	**n.s.**
Matrilineal inherit. of movables (5)	-1.49	.38	<0.0001	-.17	.41	**n.s.**
Patrilineal inherit. of land (5)	-.73	.23	0.002	-.24	.23	**n.s.**
Patrilineal inherit. of movables (5)	-1.05	.25	<0.0001	-.41	.25	**n.s.**

The model of geographical diffusion. The model of geographical transmission used to investigate the transmission of traits between populations could be made more realistic in several ways. 'Nearest neighbours' could be weighted by actual distances and by the mobility of populations. Geographical barriers to contact could also be taken into account.

Geographical diffusion is treated as statistically equivalent to independent evolution in the phylogenetic methods used in this thesis. If two traits are consistently adopted from neighbouring populations together, or if one trait is consistently adopted from neighbouring populations in association with an environmental variable, this is evidence that the two variables are functionally related (see chapter 1). However, 'real' independent evolution (or invention) may be more difficult than adopting a trait from a neighbour. The invention of writing might be an example. Different factors might predict the invention of writing, compared to its adoption from another population. For a cultural trait, being 'difficult to invent' is similar to phylogenetic constraint in biological evolution caused by the absence of relevant mutation. If a trait is difficult to invent, then distinguishing between independent evolution and geographical diffusion of this trait would be desirable when testing hypotheses in which that trait was the dependent variable. At present, phylogenetic models do not differentiate between independent evolution and geographical diffusion, because among species, for which these models were developed, traits do not diffuse and the issue does not arise.

Data quality in cross-cultural comparison. To test hypotheses comparatively, it is necessary to classify (and preferably to quantify) variables in a way which is

comparable across cultures. For cultural variables, Murdock's (1967) *Ethnographic Atlas* remains the most comprehensive source of cross-cultural data suitable for this purpose. The fact that Murdock's dataset has not been superseded in thirty years is symptomatic of a widespread lack of interest in quantitative or comparative research in social anthropology. The focus on individual cultures, and cultural relativist orientation of most social anthropology, has some important consequences for comparative research. One can rely on Murdock's data, accepting its limitations, or collate a cross-cultural dataset oneself. Using the *Ethnographic Atlas* has the advantage that data collection is rapid, and the data has been coded by an independent researcher. It is frequently claimed that Murdock's data are inaccurate, although one suspects that this claim is usually based on prejudice rather than experience of the data. Here I cannot resist quoting Hartung (1983) who said:

> I am dismayed that the life's work of G. P. Murdock, whom I think of as the father of empirical anthropology, is routinely dismissed by colleagues who are not very familiar with that work, who do not contribute to the coded data, who do not test hypotheses, and who do not cystallize their insights into testable hypotheses. In some circles the data are discredited by a consensus of rumor – the strength of the assertion that they are not good relying on the number of times the opinion is expressed.

Unless inaccuracies are systematically biased, they will act as noise in the data, increasing the likelihood of Type II errors (failure to detect a real effect) but not Type I errors (finding a spurious effect).

A more serious problem than inaccuracy is the limited nature of Murdock's cultural variables. In many cases, one would prefer the data to be more detailed. Variables are often coded as categorical variables when there is really continuous variation between

character states. The consequence is that not all the variance can be used in the analysis, increasing the likelihood of Type II errors. For example, for the analysis of wealth inheritance in Africa (chapter 5), wealth inheritance had to be coded as 'matrilineal' and 'patrilineal', whereas it would have been preferable to have had detailed data on the actual wealth transmitted to sons and daughters, from parents and other relatives. Data are often also coded as ordinal or clumped variables. Murdock's classification of polygynous marriage (none, less than 20% of marriages, more than 20% of marriages) is an obvious example (discussed in chapter 6). Similar problems occur in comparative biology.

Primary ethnographic sources can also be used to construct a cross-cultural dataset. This has the disadvantage that an independent researcher has not coded the data. Ethnographies tend to have limitations for the purposes of comparative analysis. They usually do not list attributes of cultures systematically. Often, only societal norms are recorded; the behaviour of individuals is frequently not recorded quantitatively. Despite these limitations, in my experience, it is worth using primary ethnographic sources as well as Murdock's *Ethnographic Atlas*. Primary ethnographic sources give information about cultural variables not recorded in the *Ethnographic Atlas* (for example, daughter inheritance, chapter 5). It is also easier to make an assessment of data quality from primary rather than secondary sources. In chapter 4, original sources of data on lactose digestion were consulted where possible, in order to ascertain the precise ethnic group of the sampled population, which was not recorded in previous compilations (e.g. Simoons, 1978; Flatz, 1987). This enabled populations to be matched to other sources of cross-cultural data (e.g. Murdock, 1967).

Archaeological data. Archaeological evidence can also give information about character states or environmental variables in the past. In Pagel's (1994) maximum likelihood model, certain types of archaeological information can be mapped onto the phylogeny (computer programs to do this became available after the analysis in this thesis was done). This includes information which is universally applicable, for example, the absence of farming and domesticated livestock before 10,000 BC. To do this one needs to estimate dates of nodes on the phylogeny.

To use archaeological data that is specific to a particular region or population, it is first necessary to establish that it applies to the particular ancient population represented by a higher node on the tree. For example, Liden (1995) found evidence that the Neolithic population of Scandinavia was primarily pastoralist (chapter 4). One might want to fix that node on the tree which is ancestral to modern Scandinavians to 'pastoralist'. To do this, one would first have to ascertain that the Neolithic population in Scandinavia was ancestral to modern Scandinavians. This could be done using ancient DNA, as was done for the Neolithic 'Ice Man' found on the border of the Italian and Austrian Alps. Dated at 5,100 – 5,300 years ago, this individual clusters genetically with contemporary Alpine and Northern European populations, indicating population continuity, at least from this one individual (Brown and Brown, 1994; Handt et al., 1994; Stoneking, 1995). Literate historical populations can be placed on a linguistic tree, if their language has been deciphered.

Summary. It is possible to infer past character states (in biological and cultural traits) from cross-cultural variation in the present. Populations in a cross-cultural sample are placed on a genetic or linguistic tree, used as a model of the past relationships among

populations. Past character states, at internal nodes on the tree, can be estimated from character states at the tips of the tree (in extant populations). This enables one to infer probable past character states in traits which are not preserved in the archaeological record, like wealth inheritance practices.

Reconstructing ancestral character states on a population phylogeny (i.e. a genetic or linguistic tree) enables one to test adaptive hypotheses for cross-cultural variation. On a phylogeny, one can identify cases of independent evolutionary change in characters. It is then possible to test for correlated evolutionary change among traits, or among biocultural traits and environmental variables. This enables one to control for the problem of non-independence among populations, known as Galton's problem, which bedevils cross-cultural comparison.

In this thesis, phylogenetic comparative methods were used to test adaptive hypotheses for variation in lactose digestion capacity, sexual dimorphism in stature, and the cultural co-evolution of patrilineal inheritance and pastoralism (dependence on livestock) in Africa. The transmission of these biocultural traits between populations was also investigated, and found to be mainly vertical, from 'mother' to 'daughter' populations. This result supports the application of phylogenetic comparative methods in cross-cultural comparison.

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Appendix 1 Method for calculating great-circle distances (by Rob Baulk)

Module for Microsoft Access (version 7)

```
Option Compare Database


Public Function Distance(Lat1 As Double, Long1 As Double, Lat2 As Double, Long2
As Double) As Double

Dim DiffLat, DiffLong As Double
Dim x, y, z As Double
Dim hyp, theta As Double
Const Radius = 6378.5

DiffLat = Lat1 - Lat2
If Abs(DiffLat) >= 360 Then DiffLat = DiffLat - Sgn(DiffLat) * 360
DiffLat = DiffLat * 3.141592654 / 180

DiffLong = Long1 - Long2
If Abs(DiffLong) >= 360 Then DiffLong = DiffLong - Sgn(DiffLong) * 360
DiffLong = DiffLong * 3.141592654 / 180

x = Cos(DiffLat) * Cos(DiffLong)
y = Sin(DiffLong)
z = Sin(DiffLat) * Cos(DiffLong)

hyp = Sqr((1 - x) ^ 2 + (0 - y) ^ 2 + (0 - z) ^ 2)
If hyp = 0 Then
   theta = 0
ElseIf hyp = 2 Then
   theta = 3.141592654
Else
   theta = 2 * Atn((hyp / 2) / Sqr(-(hyp / 2) * (hyp / 2) + 1))
End If

Distance = theta * Radius

End Function
```